Vocal Communication in Blue Whales (*Balaenoptera musculus*) and Noise Interference

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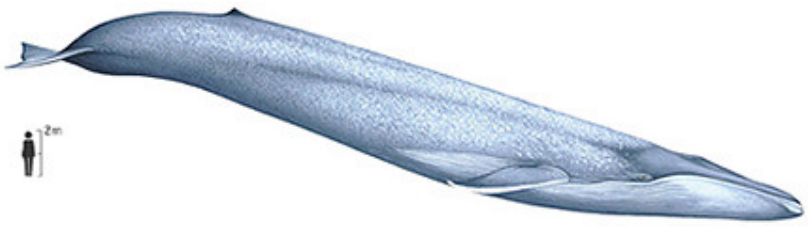

The Blue Whale

the largest animal ever to have lived. It was named 'Balaenoptera musculus' by Linnaeus (Systema Naturae, 1758) probably because of the ironic double meaning of the word 'musculus' - the Latin name for 'muscular' but also interpretable as 'little mouse'.

2009

CONTENTS

SUMMARY

Long-range acoustic communication represents one of the main modalities to transmit information and maintain social relationships among distant individuals. By examining variation in long-range signals, we can gain insights into their function as well as the processes underlying the variation. Since communication and social behaviour are tightly linked, variation in acoustic signals can reflect behavioural patterns that are important to better understand the sociobiology of a species. Moreover, changes in vocal behaviour can also be induced by factors interfering with acoustic communication, such as anthropogenic noise. In my thesis, I investigated patterns of variability in the long-range male vocal displays ('songs') of North Atlantic blue whales (*Balaenoptera musculus*) at the level of the population, the individual, as well as in relation to the social and behavioural context. I also examined whether seismic noise affected the production of blue whale 'calls', transient discrete vocalisations used by both sexes in short-range social contexts. Blue whales are invaluable for the study of variation in long-range signals because they live in a highly fluid social environment, and their songs - redundant, patterned sequences of infrasonic sounds - can be heard over hundreds of kilometres. I collected simultaneous behavioural observations and acoustic recordings in the field and analysed the temporal and acoustic structure of blue whale songs. I found that multiple features differed between the songs of blue whales from the eastern and western North Atlantic. It is thought that due to the extensive singing during their basin-wide roaming, blue whales throughout the North Atlantic may be physically and/or acoustically sympatric. The song divergence found here was likely dependent on ecological factors, but could also have been driven by mate choice. In fact, songs are thought to be male reproductive displays, suggesting that female preferences for specific traits could have accounted for the observed differences. Blue whale songs also showed inter-individual variation and may thus convey information relevant to distinguishing between singers. Considering that multiple senders can be active at the same time, individual song differences are likely used by conspecifics to assess individuals. Since blue whales roam highly dispersed, singing might play a role in mediating inter-individual interactions from a distance (e.g. mate attraction). This hypothesis was supported by the fact that songs were always produced by single steadily moving males and appeared to be directed to an unknown audience. In contrast, I found that in stationary situations (feeding, socialisation) and in the presence of females nearby, infrasonic sounds composing a song were emitted singly or in short irregular sequences (fragments). This suggests that in a stationary short-range situation, the repetition and redundancy found in songs is superfluous because potential receivers are in close physical and visual range. Fragments might suffice to indicate the presence of a signaller and efficiently transfer individual information.

Finally, I found that blue whales consistently increased call production when exposed to seismic survey activity. The observed response presumably represents a compensatory behaviour to the rise in ambient noise from the seismic survey. Increasing call production could enhance the probability of receivers to detect the signal ('information theory'). Since the response was observed at low noise levels, this finding has substantial management and conservation implications.

This thesis increases our knowledge about the use of long-range vocalizations in blue whales, particularly with respect to mate attraction and also about compensatory vocal behaviours in response to interfering anthropogenic noise. It shows that variation can occur at multiple levels of the signal and that blue whale songs are multicomponant signals that might have evolved to cope with a variable socio-ecologial environment.

ZUSAMMENFASSUNG

Langstrecken akustische Kommunikation ist das beste Mittel, um Information zwischen entfernten Individuen auszutauschen und somit soziale Verbindungen auch auf Distanz aufrecht zu erhalten. Beim Untersuchen von Variationen in Langstrecken-Signalen können wir Einsicht über die Funktion der Signale gewinnen und über die Faktoren, welche zu diesen Variationen geführt haben. Weil Kommunikation und Sozialverhalten stark miteinander verbunden sind, können Variationen in akustischen Signalen Verhaltensmuster wiederspiegeln, die wichtig sind, um die Soziobiologe einer Art besser zu verstehen. Zudem, können Veränderungen im akustischen Verhalten auch von externen Faktoren bewirkt werden, welche die akustischen Kommunikation beeinträchtigen, wie zum Beispiel anthropogener Lärm. In meiner Dissertation habe ich Variationsmuster in den Langstrecken-Signalen von nordatlantischen Blauwalmännchen (*Balaenoptera musculus*) untersucht, den sogenannten ‚Gesängen', und zwar auf der Ebene der Population, des Individuums, sowie im Zusammenhang mit dem Verhalten und dem sozialen Umfeld. Ausserdem habe ich den Einfluss von seismischem Lärm auf die Produktion von ‚Rufen' untersucht. Rufe sind flüchtige Signle, die unregelmässig erzeugt werden und im Repertoire der Männchen sowie der Weibchen vorkommen, meist bei sozialen Interaktionen. Blauwale sind interessant für Studien im Bereich von akustischen Variationen, weil sie in einem sehr veränderlichen sozialen Umfeld leben und ihre Gesänge - redundante, strukturierte Sequenzen von Infraschallsignalen – über hunderte von Kilometer gehört werden können. Ich habe gleichzeitig akustische Aufnahmen und Verhaltensdaten im Feld gesammelt sowie die zeitliche und akustische Struktur von Blauwalgesängen analysiert. Dabei habe ich festgestellt, dass die Gesänge von West- und Ost-Atlantik Blauwalen sich in mehreren Eigenschaften unterschieden. Wegen des kontinuierlichen Singens während der weitläufigen Wanderungen, sind Blauwale innerhalb des Nordatlantiks sehr wahrscheinlich akustisch oder physisch sympatrisch. Die Gesangsunterschiede waren zum Teil auf ökologische Faktoren zurück zu führen, könnten aber aufgrund von sexueller Selektion enstanden sein. Man nimmt nämlich an, dass es sich beim Blauwalgesang um ein Balzverhalten handelt. Im Falle der beobachteten Unterschiede könnten also auch weibliche Vorlieben für gewisse Gesangseigenschaften zugrunde liegen. Blauwalgesänge wiesen auch individuelle Unterschiede auf, welche Informationen beinhalten könnten, die beim Unterscheiden der Sänger relevant sein könnten. Wenn man bedenkt, dass mehrere Individuen gleichzeitg singen können, ist es plausibel, dass individuelle Unterschiede von Artsgenossen verewendet werden, um Individuen abzuschätzen. Weil Blauwale weit entfernt von einander herum ziehen, könnte das Singen bei interindividuellen Interaktionen auf Distanz eine wichtige Rolle spielen (z. Bsp. um Weibchen anzulocken). Dies wird auch dadurch bekräftigt, dass Gesänge immer von einzelnen, konstant schwimmenden Männchen erzeugt wurden und allem Anschein nach einer unbekannten Zuhörerschaft gerichtet sind. Im Gegensatz dazu wurden in stationären Situationen (Fressen, Sozialverhalten) und immer in Anwesenheit von Weibchen, Einzelnoten oder Gesangsbruchstücke produziert. Dies weist darauf hin, dass in einer stationären Situation, wo Individuen in Reichweite voneinander sind, ein repetitives Wiederholen wie bei den Gesängen nicht erforderlich ist, weil die möglichen Empfänger in der Nähe sind.

Zum Schluss, habe ich gezeigt, dass Blauwale, die seismischem Lärm ausgesetzt waren, konsistent mehr Rufe produzierten. Diese Antwortreaktion stellt möglicherweise ein Kompensationsmechanismus dar, um den Lärmeinfluss zu überwinden. Eine Rufzunahme würde die Wahrschienlichkeit erhöhen, dass Empfänger das Signal erkennen können (‚Informationstheorie'). Weil die Tiere bereits bei rlativ niedrigen Lärmwerten reagierten, könnten diese Forschungsergebnisse auch wichtige Folgen für den Artenschutz haben.

Diese Dissertation trägt zum besseren Verständnis von Langstrecken-Kommunikation bei Blauwalen bei, vor allem im Bezug auf Balzverhalten und Partnersuche, sowie von Anpassungsmechanismen, um den mit der Kommunikation interferierenden Lärm zu überwältigen. Sie zeigt auch, dass Variationen auf verschiedenen Ebenen der Signalstruktur auftreten, und dass Blauwalgesänge Multikomponenten-Signale darstellen, die sich höchstwahrscheinlich entwickelt haben, um in einem sozial sowie ökologisch variablen Lebensumfeld zurecht zu kommen.

GENERAL INTRODUCTION

Living in a fluid, dispersed network

The importance of acoustic communication in the wide-ranging blue whale *(Balaenoptera musculus)*

Photo: Denis Bouchard

"The limits of my language mean the limits of my world." L. Wittgenstein

Communication is crucial in mediating social behaviours. The social environment in which much communication occurs, is a network, in which several signallers and receivers share parts of the same active signalling space (i.e., the area in which an individual can perceive the signals of a conspecific) (McGregor, 1993; McGregor & Peake, 2000; Peake et al., 2001). When signals are long-ranging, communication occurs by definition in a network, because signals can be received over wide areas that comprise a large number of individuals. Receivers have therefore the opportunity to obtain information about conspecifics in a passive way. For example, listening to individual vocalisations or eavesdropping on acoustic interactions can be a low-cost activity to gather information about the state, quality, or fighting abilities of potential rivals or mates. This can have important implications for mate choice or future encounters (Clutton-Brock & Albon, 1979; Peake et al., 2001; Mennill et al., 2002; Fitch & Hauser, 2003; Mennill & Ratcliffe, 2004).

Fluid social systems and acoustic cues to identity

In species with no or vast territories and with a fluid social system such as elephants *Loxadonta africana*, chimpanzees *Pan troglodytes*, or dolphins *Tursiops truncatus*, acoustic communication networks play a fundamental role because individuals or units are often dispersed, out of sight, and the identity of immediate neighbours changes due to the movements of individuals and groups in relation to one another (McComb & Reby, 2005). In such an environment, long-range acoustic signalling often represents the only effective modality to transmit information for example on the location, state and attributes of a signaller. Encoding acoustic cues of group or individual identity is thus likely to be very important in maintaining social contact and coordinating movements with widely spaced group members (contact signals) (e.g., McComb et al., 2003; Mitani & Nishida, 1993; Delgado, 2006; Janik et al., 2006), or in advertising a signaller's traits (e.g., quality) to potential mates and rivals (mating signals) (Kitchen et al., 2003; Delgado, 2006; Mitra Setia & van Schaik, 2007). Furthermore, since several senders can be active at the same time, vocal identity cues might be advantageous for a receiver to recognise members of its own social unit in order to keep up with their movements or, in the case of mating signals, to locate and discriminate between individuals when facing mate choice decisions. Male vocal displays evolve as a consequence of sexual selection and individual variation in the acoustic structure of these displays are known to influence male-male competition and female choice. In a variety of organisms, a male's attributes (e.g., fighting abilities, age, rank, size, motivation) can be assessed by conspecifics in the individual structure of the mating display (Fischer et

al., 2004; McComb & Reby, 2005; Forstmeier et al., 2006), and females for example, show preferences for certain vocal traits that are related to attributes indicative of better male quality and condition (McComb, 1991; Birkhead et al., 1998; Cotton et al., 2006; Charlton et al., 2007). As a consequence, variation in the mating display affects individual reproductive success (McComb, 1991; McElligott et al., 1999; Reid et al., 2005; Schmidt et al., 2006).

Audience and signal variation

In a communication network, senders broadcast information in front of an audience. The presence of several receivers (e.g., other than the primary target receiver) as well as the composition of the audience can therefore affect signal output. Audience-specific signalling has been reported across taxa. In lions for instance, nomadic males only roar when local resident males are unlikely to hear them in order to avoid aggressions (Grinnell & McComb, 2001), or in several bird species, males use different song type categories or acoustic structures in the presence of females or males respectively (Spector, 1992; Trillo & Vehrencamp, 2005).

In the case of long-range signals, the audience can be vast and even further enhanced by the movements of individuals with respect to each other. In such a fluid system, an individual may broadcast to and receive signals from a larger section of the overall population than normally possible in territorial systems (McComb & Reby, 2005). This also implies that individuals have the potential to be acoustically sympatric with other groups or even populations of the same species, which might have implications for signal evolution, particularly if the signal is involved in reproduction (Noor, 1999; Hatch & Clark, 2004; Jang & Gerhardt, 2006; Pfennig & Ryan, 2006; Higgie & Blows, 2008). For example, if females prefer familiar reproductive displays (e.g., songs), this can lead to assortative mating and consequently group or population divergence (Chilton et al., 1990; Clayton, 1990; Marquez & Bosch, 1997; Gerhardt, 1999; Higgins & Waugaman, 2004; Higgie & Blows, 2008).

Ecological influences on acoustic communication networks

Ecological factors can also have an impact on acoustic communication networks by interfering with signal transmission. Competition for the same signalling space with other species or an increase in ambient noise for instance could disrupt communication by masking acoustic signals and potentially induce behavioural changes for coping with such interference. There is increasing concern particularly with regard to the impact of noise from human activities on highly acoustic species, including amphibians, birds, bats and cetaceans

(Richardson et al., 1995; Slabbekoorn & Peet, 2003; Brumm et al., 2004; Sun & Narins, 2005; Parks et al., 2007; Schaub et al., 2008). Ambient noise can shorten the range over which individuals can hear each other and especially in dispersed species that rely on the perception of acoustic signals also at a distance, masking by noise could result in the disruption of acoustic contact between animals (Payne & Webb, 1971; Ord & Stamps, 2008).

Cetacean acoustic communication networks with emphasis on the blue whale (Balaenoptera musculus)

The Ocean is an open-ended environment with few physical barriers. It imposes constraints on acoustic communication networks due to underwater transmssion properties, but also advantages that differ from those found in terrestrial habitats. Light penetrates the ocean only a few tens of metres, thus limiting vision, whereas sound travels five times faster underwater than in air, and consequently much further. Of all the ways to transmit information through the sea, sound is therefore the most effective one, and cetaceans take advantage of this property relying heavily on its production and perception for survival. They use sound for navigation, food detection, and social communication (e.g., maintenance of social cohesion, reproductive behaviour) (Tyack, 2000; Tyack & Clark, 2000). Although most acoustic communication is likely to occur within a network of several senders and receivers, our knowledge with respect to cetaceans is sparse. This is mainly due to the difficulty of accessing and observing whales and dolphins in the wild. Nevertheless, cetaceans are interesting for the study of communication networks because they live in large aggregations or in fluid societies in which group composition or the identity of neighbouring individuals changes frequently due to their movements in relation to one another. Furthermore, they are highly vocal, capable of social learning and have high cognitive abilities comparable with those of the great apes (Janik, 2005).

Cetacean acoustic communication networks are probably the largest worldwide (Payne & Webb, 1971). Because in the marine environment sound is the best vehicle for carrying information also over long distances, the active signalling space of cetacean vocalisations is much larger than the one of terrestrial animals. In species that rely on group-cohesion, for example to coordinate behaviours such as cooperative feeding, the long-ranging properties of their vocalisations imply that other groups of the same species might share their active signalling space and potentially interfere with within-group communication. Therefore, species that live in such stable groups such as sperm (*Physter macrocephalus*, Rendell &

Whitehead, 2003) or killer (*Orcinus orca*) whales (Ford & Fisher, 1983), often evolved group-distinctive vocal repertoires. In contrast, in species where group composition is less stable, group-specific vocalisations are not required. In these societies, in which group composition changes frequently such as in bottlenose dolphins (*Tursiops truncatus*), vocal signatures occur at the individual level (Janik, 2005). Goroup or individual recognition have been suggested to be the main selection pressures on the evolution of vocal learning in ceaceans (Janik & Slater, 1997). Vocal learning and song matching is also known to occur in a baleen whale species, the humback whale (*Megaptera novaeangliae*, Noad et al., 2000). However, the vocalisations involved are mating displays suggesting that sexual selection might also have acted on these signals. Baleen whales generally do not show stable group formations, but reproductive character displacement has been described for the songs of sympatric groups of fin whales (*Balaenoptera physalus*) within the North Atlantic (Hatch & Clark, 2004; Delarue et al., 2009). The benefits for fin whales for developing group-specific song divergence remain unknown. This is also linked to the difficulty of studying these species, in particular if pelagic (i.e., offshore) such as the fin or the blue whale.

Blue whales probably share the largest communication network of all animal species because they produce among the loudest and lowest sounds in the animal kingdom that are particularly well suited for transmission over very long distances (Cummings & Thompson, 1971; Payne & Webb, 1971; Bass & Clark, 2003). Depending on the environmental conditions (e.g., noise, temperature, salinity), blue whale infrasonic sounds can be heard at tens, several hundreds, and even thousands of kilometres, thus likely encompassing a large number of receivers (Clark, 1995; Clark & Ellison, 2003). These very large active signalling spaces probably reflect the social organisation and behaviour of blue whales.

The blue whale (Balaenoptera musculus) – the study species

Blue whales are the largest animals ever to exist on Earth. There is scarce information about their ecology, life history and sociobiology because of the difficulty to answer relevant questions about many aspects of their life. Blue whales may be found singly, often in pairs, or occasionally in small unstable groups (Sears, 2008). In areas where there is a high concentration of food (i.e., krill), large aggregations can be observed (up to 50 animals), although blue whales do not show co-operative feeding behaviour nor do they form compact, stable groups seen in other whale species (Sears, 2008). Their social environment is fluid, variable, and highly dispersed, also because blue whales are non-territorial and nomadic (Sears et al., 1990). Seasonal migrations between summer feeding and wintering grounds are

described for some populations, but not all individuals do migrate (Mate et al., 1999; Stafford et al., 2001; Sears & Calambokidis, 2002). In fact, it is assumed that blue whale distribution is largely governed by food requirements, almost year-round, which may explain their extensive roaming (Reeves & Clapham, 1998; Moore et al., 2002; Hucke-Gaete et al., 2004; Sears, 2008). Most reproductive activity (i.e., mating and calving) takes place during the winter but there is no knowledge about the existence of specific breeding or calving grounds (Mizroch et al., 1984). This is in contrast with what is known form the closely related humpback whale, that performs seasonal migrations between the same feeding and breeding grounds every year. Blue whale females typically give birth once every two to three years after a genstation period of ten to twelve months (Sears, 2008). Weaning probably occurs on, or while travelling to the summer feeding areas (Yochem & Leatherwood, 1985). Females rear their offsprings alone and because of the fast growth and rapid independence of the progeny (weaning period: 6-8 months), no group-care (e.g., allomothering behaviour) is observed as in several toothed whale species. Sexual maturity is typically reached at eight to ten years in males and around the age of five by females. In general, adult females are slightly larger males. Blue whales have a life expectancy of at least 80 years. Predation pressure is low and mainly due to killer whale attacks (Sears & Calambokidis, 2002).

Blue whales are highly vocal and males emit songs - redundant, stereotypic sequences of infrasonic units - almost year-round, with a period of highest incidence during fall through early spring (Charif & Clark, 2000; Stafford et al., 2001). Songs are supposed to be mating displays, their production can last several hours up to days, and is associated with males travelling out of sight of other individuals (Mellinger & Clark, 2003; Oleson et al., 2007). The fact that blue whales are known to range almost throughout an ocean basin (up to several thousands of kilometres) emitting very long-ranging songs has led to the speculation that they are panmictic, without mating restrictions upon individuals from different regions within an ocean basin (Clark, 1995; Clark & Gagnon, 2004). Furthermore, roaming over such extensive distances also implies encountering variable ecological environments (e.g., noise, oceanographic conditions).

The combination of the dispersed, wide-ranging nature of blue whales with occasional congregations and building of unstable groups in feeding grounds, the extensive singing behaviour of males, the changing composition of potential receivers, as well as the fact that most acoustic communication occurs “in public”, makes the blue whale a very interesting subject for investigating the factors underlying variation in vocal signals in the framework of

communication networks. In my thesis, I examine patterns of variability - in terms of temporal and acoustic structure - of North Atlantic blue whale songs at the level of the individual, the population as well as in relation to the behavioural and social context.

Outline of my thesis

When networks are large, locations of individuals difficult to predict or know, and only one sensory modality is available, it is difficult for a sender to identify who is within range as potential receiver. A possibility for the sender to overcome this problem is to broadcast information about its own identity and possibly location. Communication over long distances could for instance help coordinating behaviours or attracting potential mates. Furthermore, since asymmetry in parental investment often predicts female mate choice, information on individual differences (e.g., quality) could be extracted by females at a distance for use in reproductive decision making. In **Chapter 1,** I investigate the individual variability in song characteristics. Because songs are complex signals, I analyse multiple features, including temporal pattern, use of different song units as well as the acoustic structure of the predominant song unit type. Since different selective pressures can act at various levels of the song structure, I suggest that different song traits might encode multiple information and also serve to increase the certainty of an individual's assessment in a variable socio-ecological environment.

Within the North Atlantic Ocean, blue whales are potentially sympatric, physically or acoustically, but there is controversy about the existence of an eastern and western population (Donovan, 1991). Individuals sighted in eastern waters during the summer, have never been sighted in western water and vice versa (Sears & Calambokidis, 2002). However, it is unknown if blue whales from the two regions meet elsewhere, at other times of the year. Differences in the acoustic structure of vocalisations are known to indicate behavioural patterns relevant to understanding population structures. In **Chapter 2,** I examine the variation in the structure of the songs from the two geographical regions by analysing several song features, including composition, 'unit rate', and the acoustic structure of the predominant unit type. I suggest that differences between songs of the two geographical regions might be attributed to different factors affecting the multicomponent structure of the vocalisations.

Signal use and production can significantly be influenced by the social environment. Blue whales are often found singly and distant from other individuals, or in loose aggregations where individuals can easily see and approach each another. In **Chapter 3**, I

examine patterns of song emission, in terms of differences in the production of song units in relation to the composition of the audience (e.g., females, males present) and the behavioural context. I suggest that it is likely that song production is affected by the behaviour of the signaller as well as by the presence of a close as opposed to a distant audience.

A major concern in marine mammals is the impact of anthropogenic noise in the ocean. Ocean noise due to human activities has dramatically increased over the last 100 years, and most sounds produced are very intense and within the same frequency range used by blue and other baleen whales for vocal communication. Interference with sound production or perception (e.g., through masking) could therefore affect biologically important behaviours, isolate group members, reduce the active signalling space, and impair information transfer (Richardson et al., 1995; Ketten, 2000; Parks et al., 2007). Disruption of acoustic contact between animals that depend on acoustic signalling, could therefore have severe consequences for entire groups or populations. In **Chapter 4**, I investigate whether blue whales change their vocal behaviour during seismic surveys, and suggest that a compensatory behaviour depends on the type of signal involved as well as the behavioural context.

This thesis aims at a better understanding of long-range signalling in blue whales and and at comparing this system with other species that live in vast and fluid social environments. By putting the emphasis on communication networks, this study contributes to better comprehend the significance of patterns of variability in long-range acoustic signals at different levels of the social environment: from the individual to the group, and up to the population level. It therefore provides a more global picture of the potential role of song production in a wide-ranging baleen whale. Information of this kind, is also of importance with respect to management and conservation. Furthermore, this thesis helps to increase our knowledge about the impact of man-made noise on acoustic communication in a baleen whale, as well as the behavioural strategies that these animals use to compensate such interference. This study puts the basis for further investigations aiming at unravelling the multiple open questions about underwater communication in fluid, dispersed whale species.

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CHAPTER 1

Patterns of variability in the song of blue whales as cues for potential individual assessment

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Patterns of variability in the song of blue whales as cues for potential individual assessment

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ABSTRACT

The evolution of identity information is favoured when differentiation or discrimination of individuals is propitious. Acoustic signatures are of advantage in fluid social systems, where the location and identity of individuals are difficult to know, and multiple senders can be active at the same time. Little is known about acoustic identity in mating signals of nomadic, dispersed, non-territorial, non-gregarious species such as the blue whale *(Balaenoptera musculus)*. Mainly while travelling, males produce redundant, stereotypic songs that likely represent long-range advertisement displays. We investigated patterns of individual variability in the structure of blue whale songs in terms of unit use, temporal pattern and acoustic structure of the predominant song unit type. We also analysed within- and between-individual variation in the different song parameters and quantified the potential of each component to carry information about individual identity. Almost all analysed song features revealed individual distinctiveness. Furthermore, temporal parameters showed high within-individual variability whereas fundamental frequency, maximum contour frequency, and duration showed highest within-individual stability. These frequency variables were also the ones contributing most to separating individual song units with discriminant function analysis, accounting for 77.6% of the variability between individuals. Our results suggest that individual information is conveyed at different levels of the blue whale song structure. Such a multiple-component signal might have evolved to allow to distinguish and assess individuals more reliably and efficiently in the variable social and ecological environment blue whales live in. This might be required to promote inter-individual interactions, in particular in relation to mate choice.

INTRODUCTION

Individual variation in signals is caused by morphological differences of senders. However, these variations may be enhanced by selection if signatures facilitate identification, discrimination or assessment by receivers and are advantageous for both of them (Johnstone, 1997). The ability to distinguish between individuals is likely to be very useful in fluid social systems, where individuals move freely with respect to each other and mainly rely on one sensory modality - acoustic signalling - to transmit information also at long ranges (c.f., McComb & Reby, 2005). In such a fluid network, encoding acoustic cues to identity can be advantageous to establish social contact and coordinate movements with distant group members (contact signals) (e.g., Harrington & Mech, 1979; Mitani & Nishida, 1993; Rendall et al., 1996; Janik & Slater, 1998; McComb et al., 2000), as well as to advertise a signaller's location or attributes to potential mates and rivals (mating signals) (Fischer et al., 2004; Delgado, 2006). Furthermore, when several signallers are active at the same time and the risk of costly confusion is high, selection would further act on enhancing individual vocal distinctiveness (Jouventin et al., 1999; Charrier et al., 2001; Van Opzeeland & Van Parijs, 2004; Gwilliam et al., 2008). This would in turn increase the ability of receivers to distinguish between signallers and thus their efficiency in, for example, keeping track of conspecifics' movements or making decisions in relation to mate choice.

In some of the species with fluid, dispersed social systems, the signals involved in long-range communication are male vocal displays (Delgado, 2006). Since such displays evolve as a consequence of sexual selection, individual variation in the structure of these signals can also influence male-male competition and female choice. Individual characteristics of male mating displays can be one of the most important factors that determine male mating success (Andersson, 1994). In fact, in a variety of taxa it has been shown that conspecifics are able to assess a male's attributes (e.g., quality, fighting abilities, age, rank, size, fitness motivation) from the individual structure of their mating displays, and that different components of the display (e.g., frequency and temporal parameters) may convey distinct or related information about such cues (Gerhardt, 1992; Galeotti et al., 1997; Otter et al., 1999; Mennill et al., 2002; Fischer et al., 2004; Forstmeier et al., 2006; Castellano & Rosso, 2007; Charlton et al., 2007; Vannoni & McElligott, 2008; Koren & Geffen, 2009). Furthermore, when acoustic signalling is the only modality to assess individuals also at a distance and several males can sing at the

same time, conveying multiple individual information in the song could reduce assessment costs and thus mate-choice errors (Candolin, 2003).

Acoustic signatures of species living in fluid social systems have mainly been studied in the long-distance calls of mammals with fission-fusion patterns such as elephants *Loxadonta africana* (Poole, 1999; McComb et al., 2000; Soltis et al., 2005), spotted hyaenas *Crocuta crocuta* (East & Hofer, 1991; Holekamp et al., 1999; Theis et al., 2007) primates (Chapman & Weary, 1990; Arcadi et al., 1998), or dolphins (Sayigh et al., 1999; Janik et al., 2006). Little is known about the functional significance of individual vocalisations for species where adult males are not gregarious and roam freely (e.g., the orangutan *Pongo spp.*; van Schaik, 1999; Mitra Setia & van Schaik, 2007; Lameira & Wich, 2008). To our knowledge, individual vocal variation has never been investigated in any nomadic and highly vocal Balaenopterid whale species.

The blue whale (*Balaenoptera musculus*) is a valuable subject for the study of individual variability in acoustic signals because it lives in a very dispersed and fluid social environment in which no long-term stable groups are formed and males emit, almost year-round, redundant, stereotypic sequences of infrasonic sounds (songs) (Cummings & Thompson, 1971; Mellinger & Clark, 2003; Oleson et al., 2007). Singing occurs mainly while travelling out of sight of other conspecifics (chapter 3; Clark, 1995; Oleson et al., 2007), and blue whales are known to range widely, up to several thousands of kilometres (Clark, 1995). The acoustic structure, i.e., infrasonic, long units repeated over several hours up to days, makes songs well suited to be transmitted over long distances in a marine environment (Bass & Clark, 2003; Clark & Ellison, 2003). Singers can potentially be heard by other individuals at ranges of at least several hundreds of kilometres in their main habitat, the deep sea environment (Clark & Ellison, 2003). Consequently, communication occurs in a potentially huge network of multiple signallers and receivers. The function of songs still has to be elucidated, but there is strong evidence that they represent mating displays (chapter 3; Tyack & Clark, 2000; Oleson et al., 2007).

While roaming, due to the movements of individuals in relation to one another, the distances between senders and receivers are highly variable. Since acoustic signals attenuate and degrade during transmission, their information content might be affected (Fig. 1) (Naguib & Wiley, 2001; Naguib et al., 2008; Luther & Wiley, 2009). Furthermore, a signaller does not constantly know who is at which distance as potential receiver. Consequently, an individual

might overcome these problems by conveying identity information in multiple song components and thus enhance detection, differentiation and potentially discrimination of a signal in a variable environment (Rowe, 1999; Candolin, 2003).

Under these socio-ecological circumstances, individual vocal identity might play an important role in mediating social interactions in the blue whale. Therefore, in this study, we examined the issue of individual identity in the song of blue whales by analysing the variability of multiple structural features of their songs, including temporal pattern, use of different song units and the acoustic structure of the predominant unit type. Furthermore, we determined the relative contribution of each acoustic unit variable in discriminating between individuals. Finally, since blue whale songs are likely to be affected by multiple selective forces, we discussed the results with respect to potential functional hypotheses of complex signalling (i.e., use of multiple components) and to the individual information potentially available to receivers.

METHODS

Study Site and Subjects

The study was carried out in the St. Lawrence Estuary, Qc. Canada (western North Atlantic, 49.5 N, -69.0 E) from July to October 2003 to 2005. During this period, a portion of the North Atlantic blue whales aggregate in this feeding ground (Sears et al. 1990). In early autumn, in coincidence with the approaching breeding season and the formation of female-male pairs, blue whale males start to emit songs (chapter 3), which then persist for several months with a period of highest occurrence between autumn and early spring (Charif & Clark, 2000; Stafford et al., 2001). Blue whales can be recognised by the pigmentation on their flanks and most of the animals present in the study area are listed in a photo-identification catalogue for the western North Atlantic (Sears et al., 1990) and can thus be individually identified.

Acoustic Recordings and Data Processing

Acoustic recordings were made using an array of autonomous bottom-moored recording units referred to as “pop-ups” (Cornell University, Bioacoustics Research Program (CUBRP), Ithaca, NY, USA) (Clark et al. 2002, Clark and Clapham 2004). In 2003 we used three MARUs that recorded continuously at a sampling rate of 2kHz. In both 2004 and 2005, we deployed five units that recorded continuously at 1kHz. Prior to deployment, we synchronised

the units at GPS time (GMT-05:00) to correct for clock drift in the system as well as precise synchronisation of multiple units in an array. The units were placed 1.5 - 2 km apart in a triangular or “W”-pattern, depending on their number, at depths between 60 and 100m. Throughout the recording season, during periods with no animal sightings, we collected GPS positions of known sound sources (e.g., light bulb breaks), which were used to validate the location accuracy of the array.

We decimated all recordings to a sampling rate of 1kHz to allow a direct comparison between all recordings. Acoustic data were visualised as continuous 24h-spectrograms using XBAT version 6.1.0.1, a specialised acoustic analysis program written in MATLAB (version 7.0.4, release 13, The Mathworks, Natick, Massachusetts, USA) developed by the CUBRP (Figueroa & Robbins 2008); www.xbat.org). Songs were identified using the automated "Data Template Detector", an XBAT routine written by H. Figueroa (CUBRP), which looks at the time cross-correlation sequence between an example event and the sound, and creates events corresponding to the significant peaks (www.xbat.org, Brandes et al. 2006). From visual inspections of the detections, we chose only song sequences for the analysis that had a signal-to-noise ratio sufficient to accurately measure all acoustic variables. The units in a song had to feature at least one harmonic and all the spectral contours of the units had to be distinctive. We used standardised display settings to reduce variation in the accuracy of the frequency and time resolution. Spectrograms were calculated by Fast Fourier Transform (FFT size: 2048 points; Hanning window; window size: 2.1s with 80% overlap). Locations of singing whales were calculated from the arrival-time differences of their vocalisations as recorded on different recording units in the array using an XBAT extension (Cortopassi & Fristrup 2005).

Identification of Individual Songs

Simultaneously with the recordings, we also conducted boat-based visual observations using a 7m rigid-hulled inflatable boat. For each whale encountered in the pop-up recording area, we noted the number of whales, time, and position of each animal in sight at each surfacing after a dive. At the same time, we used a focal sampling procedure for individual whales to record the GPS positions of the individual’s dive (seen as a distinctive swirl at the ocean surface at the place where the whale dived) and to take photos of the animal’s body coloration pattern and markings for later confirmation of the individual’s identity. We attempted to get photo-ids of all animals present during an observation day. When possible, we conducted focal follows of each animal (usually between 1 and 6) within the visible range of the boat in the pop-up area. The duration of these focal observations comprised either three to five surfacing periods,

defined as blow cycles, or 30min to 1h in case the animals were feeding at the surface (no long deep dives). This enabled us to match the GPS track of an individual at the surface with its acoustic track below the surface. This procedure was applied to ensure that the identities of the individuals included in the analysis were known.).

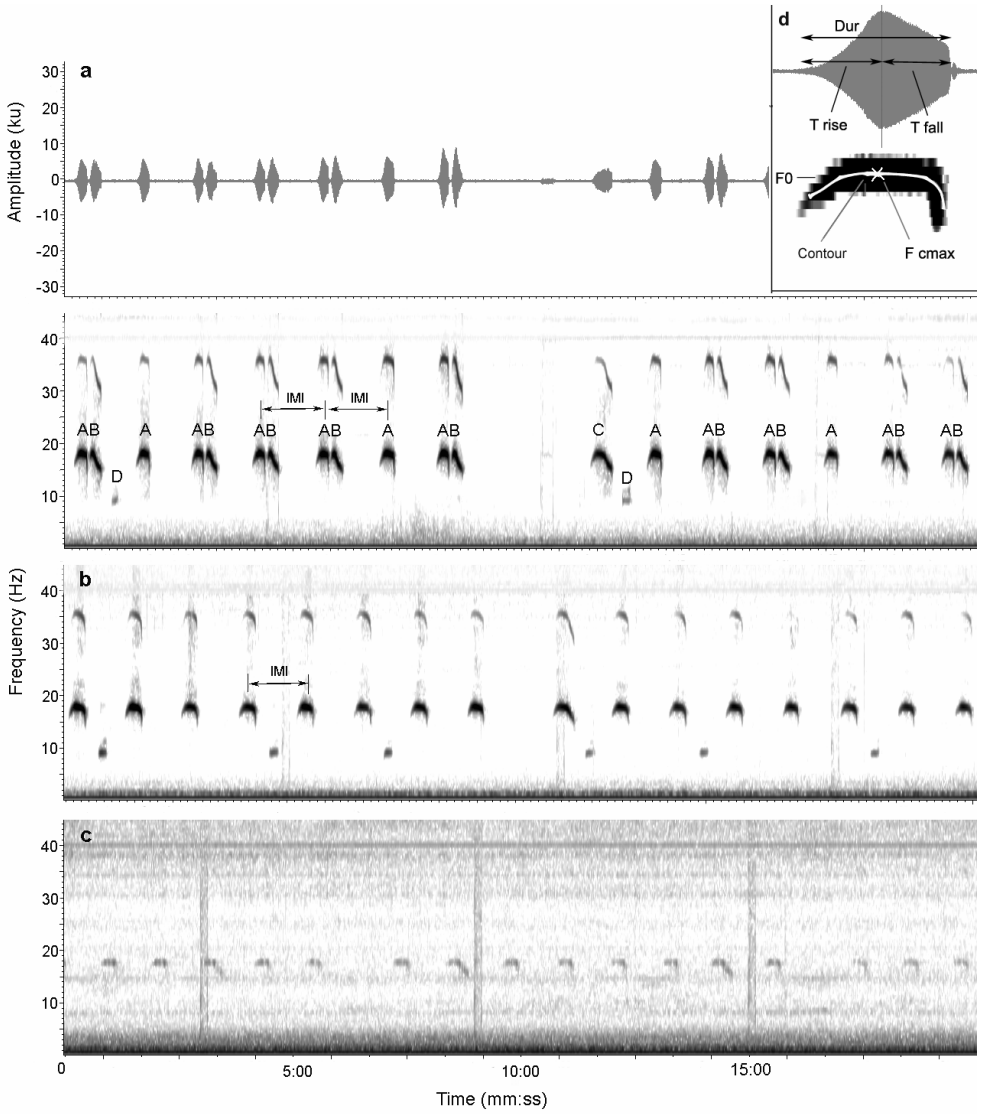

Fig. 1 The two types of North Atlantic blue whale songs. **(a)** waveform and spectrogram of a type 2 song (with regular occurrence of downsweep units), **(b)** spectrogram of a type 1 song (with < 6% or no downsweep unit), **(c)** spectrogram of a song far away (exact distance unknown). The four North Atlantic unit types are: monotonic (A), downsweep (B), hybrid (C) and 9-Hz (D) unit. IMI represent inter-monotonic interval examples. The monotonic-downsweep pair is indicated with AB. **(d)** Monotonic call type magnification showing the frequency contour (white line) and five of the six variables measured: duration (Dur), rise time (T_{rise}), fall time (T_{fall}) measured from the waveform, fundamental frequency (F_0) , maximum contour frequency (F_{Cmax}, cross). The sixth variable C_{grad} cannot be illustrated in a graph.

Song Structure Analyses

Song Unit Use

The blue whale song in the North Atlantic is composed of up to four different infrasonic sound types: monotonic, downsweep, hybrid, and 9-Hz units (Edds, 1982; Mellinger & Clark 2003; Berchok et al., 2006) (Fig. 1). Units are combined into phrases which are repeated to form a song (described in Mellinger & Clark, 2003). There appears to be a high level of stereotypy in the order in which units are produced within a phrase, although not all unit types necessarily occur in a song. Monotonic units are the predominant ones, present in every song. The downsweep occurs always in pair with a montonic unit and the hybrid unit is a combined monotonic and downsweep unit (Berchok et al., 2006) that often occurs at the beginning of a phrase. The 9-Hz unit often follows hybrid units but can also occur after other unit types (Mellinger & Clark, 2003). We identified unit types by visual inspection of the spectrogram (Fig. 1a/b) and counted the number of each unit type in the first hour of each individual song.

Temporal Pattern

We determined intervals between monotonic units and rates of song unit production for each individual song. Inter-monotonic intervals (IMI) were calculated using the absolute differences of the centre times of consecutive monotonic units that were measured in XBAT using the frequency contour measurement extension (Cortopassi, 2004) (Fig. 1). We only included IMI within a sequence, excluding the long intervals between sequences that likely correspond to respiration breaks (Mellinger & Clark, 2003). Furthermore, because the presence of downsweep units might influence IMI, we defined type 1 songs without downsweep units (≤ 6% downsweep units) and type 2 songs with downsweep units within a song (Fig. 1). For the unit rate analysis we divided each song into 5-minute samples and counted the number of all types of units per 5-minute sample.

Acoustic Structure

We measured spectral and temporal acoustic variables only of monotonic units that were not immediately followed by a downsweep unit, because it was the unit type present in all songs. We used ten randomly chosen high-quality monotonic units per individual song. We measured three temporal and three spectral variables from a monotonic unit's fundamental frequency contour. The temporal variables were duration (Dur), rise time (T_{rise}) and fall time (T_{fall}), measured from the waveform in Raven Pro (version 1.3. CBRP, Ithaca, NY) (Fig. 1).

The spectral variables included fundamental frequency (F_0), maximum contour frequency (F_{Cmax}), and average contour gradient (C_{grad}), measured from an energy envelope containing 95% of the unit's energy using the frequency contour measurement extension in XBAT (FFT size: 2048 points; Hanning window; window size: 2.1s with 80% overlap, number of points for contour measurements: 80) (Cortopassi, 2004) (Fig. 1). Fundamental frequency was calculated as the average of the values of the fundamental frequency along the contour (at 80 different points). The contour gradient was obtained by calculating the mean of the absolute value of the derivatives at each point of the contour (Fig. 1). This measurement indicates on average how much change there is in the contour over time (unit: Hz/s).

Statistical Analysis

Within and Between-Individual Variation

To describe the amount of variability in song parameters, we calculated variance components within and between individuals. Table 1 summarises the parameters used for each individual song. After confirming that ANOVA assumptions were met, we obtained the variance components for all acoustic variables as well as for IMI and unit rate by using a linear mixed-effects model (LMM) procedure fitted with residual maximum likelihood estimation (REML, lme and VarCorr functions) (Pinheiro & Bates, 2000). We conducted an univariate LMM with individuals as random factor. This procedure provided estimates of within- and between-individual variance components (VC_w and VC_b). We also expressed each variance component as a percentage of the sum of all variance components in order to give a measure of the relative strength of variation for any given variable ($100\% * VC_w / (VC_w + VC_b)$ and $100\% * VC_b / (VC_w + VC_b)$). The analyses were performed in R 2.7.1 (R Development Core Team 2008).

Song Unit Use and Temporal Pattern

We performed a Chi-Square test to compare proportions of unit type occurrence between individuals in one hour of song. This analysis revealed whether individuals differed in unit use. For the comparison of the IMI between individuals, we computed a nested ANOVA with individuals nested in song type (IMI: 359, 73.6±4.7 IMI per individual per song type1, 75.1±2.2 IMI per individual per song type2, N=9). To examine the individual variability in unit rates, we performed a Kruskal-Wallis test using eight randomly chosen 5-minute samples per individual (Unit rate: 64, 8 per individual, N=8). These statistical analysis were also performed in R.

Table 1 Means ± standard deviation per individual for all measured acoustic variables of 10 randomly chosen monotonic units, inter-monotonoic intervals (IMI), and unit rates (UR) per individual.

Individual	Date	Dur (s)	T_{rise} (s)	T_{fall} (s)	F_{Cmax} (Hz)	F_0 (Hz)	C_{grad} (Hz/s)	UR (units/5-min)	IMI (s)
1†	9 Oct 2003	16.48± 0.70 (10)	7.50±0.83 (10)	8.99±0.76 (10)	17.95±0.05 (10)	17.79±0.03 (10)	0.18±0.02 (10)	6.75±0.88 (8)	76.79±4.58 (48)
2†	24 Aug 2004	18.43±0.84 (10)	9.43±0.50 (10)	9.00±1.00 (10)	17.98±0.02 (10)	17.81±0.04 (10)	0.19±0.01 (10)	8.00±1.51 (8)	76.68±5.05 (29)
3†‡	4 Sep 2004	16.61±0.77 (10)	9.72±0.73 (10)	6.89±1.05 (10)	17.83±0.02 (10)	17.69±0.02 (10)	0.16±0.01 (10)	— —	74.58±4.76 (15)
4	8 Sep 2004	17.58 ±1.04 (10)	11.40±1.26 (10)	6.22±0.84 (10)	17.82±0.01 (10)	17.67±0.03 (10)	0.17±0.02 (10)	6.44±0.73 (8)	74.80±3.54 (50)
5	5 Oct 2004	18.11±0.66 (10)	9.28±1.31 (10)	8.83±1.25 (10)	17.85±0.02 (10)	17.69±0.02 (10)	0.17±0.01 (10)	6.13±0.64 (8)	71.63±4.46 (46)
6	4 Sep 2005	21.30±0.60 (10)	11.15±1.70 (10)	10.15±1.63 (10)	17.77±0.02 (10)	17.60±0.03 (10)	0.13±0.01 (10)	6.5±0.53 (8)	75.16±2.37 (41)
7	9 Sep 2005	17.40±2.09 (10)	9.70±1.08 (10)	7.68±1.76 (10)	17.91±0.05 (10)	17.77±0.04 (10)	0.17±0.03 (10)	6.00±0.53 (8)	68.60±4.85 (35)
8†	10 Sep2005	16.60±1.25 (10)	9.35±2.09 (10)	7.18±2.50 (10)	17.89±0.03 (10)	17.71±0.06 (10)	0.17±0.03 (10)	5.75±0.89 (8)	72.39±6.28 (56)
9	15 Sep 2005	21.50±0.91 (10)	11.56±2.05 (10)	9.97±1.69 (10)	17.76±0.02 (10)	17.54±0.04 (10)	0.14±0.01 (10)	6.25±0.46 (8)	78.00±2.64 (39)

Numbers in brackets indicate the number of samples per individual. † type 2 songs (with downsweep units). ‡ individual not used for the unit use and unit rate analysis because of insufficient song length.

Acoustic Structure

To test for individual effects on the acoustic variables, we performed for each variable a univariate ANOVA (Variable: 90, 10 variables per individual, N=9). After graphically assessing multivariate normality and homogeneity of variances in R, we carried out cross-validated discriminant function analysis (DFA) using SPSS 16 (SPSS Inc., Chicago, IL, USA) to examine variation in the acoustic variables of monotonic song units across individuals. DFA is useful for building a predictive model of group membership based on observed characteristics. In addition, it allows estimating which parameters contribute most to the separation (Tabachnick & Fidell, 2001). DFA generates canonical discriminant functions represented by the linear combination of the acoustic variables that maximally separate units into individuals. The discriminant functions are used to classify each monotonic unit to a

particular individual and the percentage of units correctly assigned gives an estimate of how well individuals can be distinguished based on these linear combinations of the acoustical variables. We assessed the classification error using the leave-one-out cross-validation, in which one case is left out of the training set and then used as a test set. Repeated for all the cases in the data set, this yields an estimate of the accuracy of the method and is particularly appropriate when sample sizes are small; (Goutte, 1997; McGarigal et al., 2000; Lachlan & Servedio, 2004; Vannoni & McElligott, 2007). From the structure matrix we identified which variables contributed most to individual discrimination. A variable entered the analysis if its minimum tolerance was 0.001, with tolerance defined as the proportion of its within-groups variance not accounted for by other variables in the analysis (Dempster, 1969). A variable with very low tolerance is nearly a linear function of the other variables; its inclusion in the analysis would make the calculations unstable. Since T_{fall} did not pass this tolerance criterium, it was excluded from the analysis.

RESULTS

Identification of Individual Songs

We obtained six cases where we could match GPS surface tracks from the focal follows with acoustic tracks. Since the focal surface animal was not always the singer, we increased the sample size by using a second method. Comparing photo-id pictures of the whales present, we selected three additional song samples from survey days in which none of the blue whales already chosen with the first method was sighted, and in which distinct animals were present (i.e., three days with different “sets” of blue whales). For all but two analyses we used nine high-quality songs. Because one individual produced a song that lasted only approx. 30 minutes, we had to exclude it from the analysis of song unit use and unit rate (metric: first hour of song).

Within- and Between-Individual Variation

Four song components differed markedly between individuals, whereas four varied greatly within individuals. Dur, F_0, F_{Cmax}, and C_{grad} showed greater between-individual than within-individual variation (stable properties), whereas T_{rise} and T_{fall} , IMI and unit rate showed greater within- than between-individual variation (dynamic properties) (Table 2).

Table 2 Within-individual and between-individual variation coefficients (VC_w and VC_b) and relative strength (%) for the acoustic variables calculated from nine individual males (10 units per individual), for inter-monotonic intervals (IMI) (N=359, 9 individuals) and unit rates (UR) (N=64, 8 individuals).

Parameters	VC_b	VC_w	Rel strength VC_b %	Rel strength VC_w %	VC_b/VC_w	$F_{(b)}$
Dur	3.645	1.125	76.42	23.58	**3.24**	33.40*
T_{rise}	1.458	1.937	42.94	57.06	0.75	8.53*
T_{fall}	1.703	2.235	43.24	56.76	0.76	8.62*
F_0	0.008	0.001	88.24	11.76	**7.50**	54.04*
F_{Cmax}	0.005	0.001	84.14	15.86	**5.30**	11.50*
C_{grad}	0.00035	0.00033	51.21	48.79	**1.05**	76.00*
IMI	8.242	19.955	29.22	70.77	0.55	1.541
UR	0.388	0.698	35.73	64.27	0.413	5.171†*

In bold are the variables with higher between- than within-individual variation ($VC_b/VC_w > 1$). F_b: F values for the univariate ANOVAs for all acoustic variables as well as from the nested ANOVA for IMIs with * $P < 0.001$. † χ^2 for UR (Kruskal-Wallis test). $F_{(b)}$ degrees of freedom: acoustic variables (8, 89); IMI (7, 356); χ^2: UR (7, 63).

Song Unit Use and Temporal Pattern in Songs

Of the nine singers, five sang type 1 song and four sang type 2 song (Table 1). Overall, singers produced mainly monotonic units (68.3% of all units), followed by 9Hz units (15.3%), downsweep units (10.9%) and hybrid units (5.5%) (Fig. 2). Individuals significantly differed in the percentage of unit type occurrence (N = 622, d.f. = 21, Pearson $\chi^2 = 156.03$, $P < 0.0001$) (Table 3). There was no significant difference in IMI between individuals (N = 359, d.f. = 356, F = 1.541, P = 0.22) but singers differed in the number of units per 5-minute sample (unit rate) (N = 64, d.f. = 7, $\chi^2 = 18.68$, P = 0.009) (Table 2).

Acoustic Structure

Individual variation was found for all acoustic variables measured from monotonic units (Table 2). Five significant discriminant functions were generated (Table 4). Fundamental frequency and maximum contour frequency correlated with the first function and accounted for 77.6 % of the total between-individual variation. Duration was the only variable correlating with the second function that accounted for 16.3 % of the total variation. The remaining discriminant functions contributed little to the discrimination between singers (6.1 %) (Table 4). Cross-validated DFA using only uncorrelated acoustic variables classified 62.2% of the singer's monotonic units correctly (77.8% without cross-validation) compared to 11.1% expected by chance.

Table 3 Percentage of unit type occurrence per individual. One individual (ID 3) is missing because of insufficient song length.

			Unit type			
			9Hz	Downsweep	Hybrid	Monotonic
Individual	1	Count	1	33	5	55
		% within Individual	1.10%	35.10%	5.30%	58.50%
		% of Total	0.20%	5.30%	0.80%	8.80%
	2	Count	10	17	5	36
		% within Individual	14.70%	25.00%	7.40%	52.90%
		% of Total	1.60%	2.70%	0.80%	5.80%
	4	Count	21	4	7	60
		% within Individual	22.80%	4.30%	7.60%	65.20%
		% of Total	3.40%	0.60%	1.10%	9.60%
	5	Count	11	5	13	66
		% within Individual	11.60%	5.30%	13.70%	69.50%
		% of Total	1.80%	0.80%	2.10%	10.60%
	6	Count	21	0	3	46
		% within Individual	30.00%	0.00%	4.30%	65.70%
		% of Total	3.40%	0.00%	0.50%	7.40%
	7	Count	11	0	0	42
		% within Individual	20.80%	0.00%	0.00%	79.20%
		% of Total	1.80 %	0.00%	0.00%	6.80%
	8	Count	5	9	1	73
		% within Individual	5.70%	10.20%	1.10%	83.00%
		% of Total	0.80%	1.40%	0.20%	11.70%
	9	Count	15	0	0	47
		% within Individual	24.20%	0.00%	0.00%	75.80%
		% of Total	2.40%	0.00%	0.00%	7.60%
	Total	Count	102	72	37	444
		% of Total	15.30%	10.90%	5.50%	68.30%

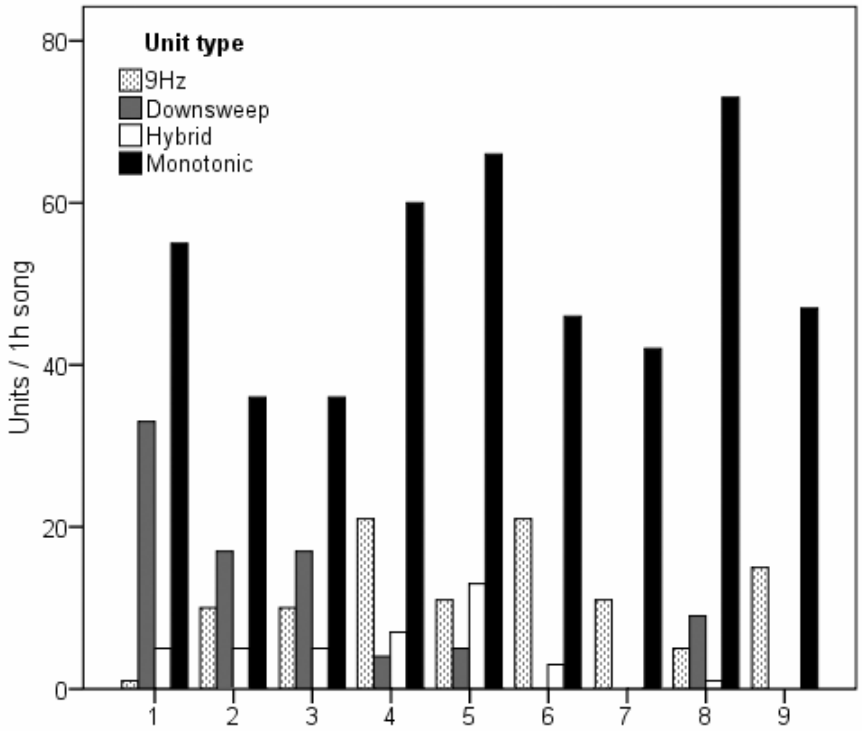

Fig. 2. Individual unit use represented as the number of different unit types (different patterns) per 1h song for each of the nine individuals. Individual 3 was excluded from the analysis because of insufficient song length.

Table 4 Structure matrix from the DFA calculated using five monotonic unit variables. The matrix shows the correlations between the variables and the discriminant functions and thus the relative contribution of each variable to the separation of individuals.

	Functions				
Variables	1	2	3	4	5
F_0	**.770**	.016	.158	-.617	.005
F_{Cmax}	**.719**	.301	-.095	.427	-.449
Dur	-.416	**.729**	.542	.002	-.030
T_{rise}	-.213	-.227	**.818**	.347	-.337
C_{grad}	.301	-.112	.095	.492	**.803**
Eigenvalue	10.294	2.166	0.477	0.263	0.067
% Variance explained	77.6	16.3	3.6	2.0	0.5

Bold types indicating largest absolute correlation between each variable and any discriminant function (r = 0.7). Abbreviations: Duration (Dur), rise time (T_{rise}), rise time (T_{rise}), fundamental frequency (F_0), maximum contour frequency (F_{Cmax}).

DISCUSSION

The aim of this study was to investigate the acoustic basis of individual identity in blue whales and to formulate hypotheses about the potential information available to receivers. Clear individual differences were found in multiple traits of blue whale songs. Cross-validated DFA assigned monotonic units to the correct individual 5.6 times better than expected by chance, suggesting that blue whale males have distinct individual acoustic characteristics in their predominant song unit type. Furthermore, except for inter-monotonic intervals, all song properties examined showed clear between-individual variability, including song unit use (i.e., proportional use of different unit types), unit rate as well as all frequency and temporal parameters of the monotonic unit. These findings suggest that all these song features represent characteristics that conspecifics could use to distinguish singing males. Consequently, blue whale songs are complex signals (Candolin, 2003; Hebets & Papaj, 2005) composed of multiple components that likely serve to transmit multiple information about the sender.

The use of multiple-component signals may provide more reliable information for receivers (Rowe, 1999). In the case of mating displays, in particular courtship signals, it may be to the signaller's benefit to provide a potential mate with information about its identity, quality and location ('content-based hypothesis'), and to transmit the information with high efficiency through the environment ('eficiency-based hypothesis') (Guilford & Dawkins, 1991; Hebets & Papaj, 2005). Blue whale song units are repeated in sequences, sequences in songs, and songs in bouts (Mellinger & Clark, 2003). This high redundancy and repetition enables a consistent transmission of information and allows receivers to locate a singer, also while travelling (Clark & Ellison, 2003). However, in order to transmit information that allows to distinguish between individuals also at long, variable distances and in changing environmental conditions (e.g., ambient noise), song traits with high propagation properties need to be highly stable (Bradbury & Vehrencamp, 1998). This study shows that duration, fundamental frequency as well as parameters describing unit modulation showed low within-individual variation and thus represent 'static' (Gerhardt, 1992), stable properties. Fundamental frequency in particular could be a useful identification feature also at considerable distances because it propagates well in the typical blue whale habitat (Bass & Clark, 2003) (Fig. 1). Furthermore, since song units are pure tones that lack almost any broadband structure (Mellinger & Clark, 2003; Berchok et al., 2006), it is likely that individual information is primarily encoded in the contour of the fundamental frequency of a

unit. However, it needs to be tested how much individual information actually remains encoded in the acoustic structure of units at long distances. This could be examined by measuring the acoustic variables in units from the same singer recorded at short and long distances to see whether song units can be correctly assigned to the sender over different ranges. Nevertheless, traits that are stable over long ranges are only a fraction of a complex signal and thus only partly represent the signaller. It is therefore questionable whether these features alone are enough to identify or assess individuals (McComb et al., 2003; Hebets & Papaj, 2005). They might however suffice to initiate social interactions at a distance, keep track of travelling males, or indicate an individual's position or swimming direction while roaming.

The combination of multiple song components might increase the ability of receivers to both better distinguish between singers and assess individuals. In anurans for instance, frequency and pulse rate have been described as static properties of their advertisement displays and found to encode information important for individual and species recognition. In contrast, the number of calls per bout, defined as 'dynamic', variable properties (Gerhardt, 1992) were found to play a major role in female choice (e.g., Gerhardt, 1992; Castellano & Giacoma, 1998; Castellano & Rosso, 2006). This implies that different song components provide different types of information about the signaller, important to assess individual males. Furthermore, static properties have been related to the past condition and viability of the signaller, whereas dynamic properties to the present condition and motivational state (Bee & Gerhardt, 2001; Scheuber et al., 2004; Jacot et al., 2007; van Dongen & Mulder, 2008).

Calling rate provides a reliable cue of motivation and fitness condition of individual signallers as shown in different species (Birkhead et al., 1998; McElligott et al., 1999; Holzer et al., 2003; Cotton et al., 2006; Schmidt et al., 2006; Zuk et al., 2008; Koren & Geffen, 2009). In this study, we found that temporal parameters such as inter-monotonic interval and unit rate showed higher within-individual than between-individual variation and thus represent dynamic properties. Furthermore there were clear differences in unit rates between individual blue whale songs. Blue whale males are known to sing over several hours up to days almost continuously, mainly while travelling (Clark, 1995). Although they might decrease the costs of song production by singing at the depths of neutral buoyancy (Williams et al., 2000; Oleson et al., 2007), differences in the number of units produced per time interval might be indicative for a male's current condition, particularly when combined with a physical activity. A correlation between differences in acoustic features, condition and

exhaustion has for example been found in baboons (*Papio cynocephalus ursinus*, Fischer et al., 2004) and in bats (*Saccopteryx bilineata*, Behr & Helversen, 2004) and suggested to represent honest advertisement cues (Zahavi, 1975; Lailvaux & Irschick, 2006). Moreover, the high inter-individual variability of the temporal parameters might underlie different motivational states (e.g., McElligott et al., 1999; Kajikawa & Hasegawa, 2000; van Dongen & Mulder, 2008).

Blue whale singers also showed clear between-individual differences in unit use. Some individuals produced all unit types whereas others produced only two. Individuals also differed in the proportion of the different unit types occurring in their songs, suggesting differences in song diversity (Fig. 2). Large syllable or element size are proper to courtship displays (Bradbury & Vehrencamp, 1998). In birds and bats for instance, syllable or element richness and diversity has been shown to correlate with mating success, extra-pair paternity and genetic diversity (Hasselquist, 1994; Marshall et al., 2003; Gil & Slater, 2000; Davidson & Wilkinson, 2004; Reid et al., 2005). Furthermore, certain syllables that are more difficult to produce are preferred by females, eliciting higher levels of sexual display (e.g., Vallet et al., 1998).

Our findings suggest that individual blue whales can be distinguished based on multiple features at different structural levels of their songs. They also indicate that multiple information is potentially conveyed in the display. Consequently, the song of blue whales represents a complex signal where patterns of individual variability might be critical for transmitting information in variable social contexts and environmental conditions. Altogether, this could increase the certainty of an individual's assessment, which is of primary importance considering that acoustic signalling is the only means of communication. Across species, complex acoustic signals are used in reproductive decision making, and multiple studies have demonstrated that different traits important for the assessment of a male (i.e., size, rank, age, reproductive success, stamina, hormonal level) are encoded in distinct structural features of the displays, in terms of the acoustic structure of calls or song units, the repertoire, and the temporal characteristics (Gerhardt, 1992; Galeotti et al., 1997; McComb et al., 2003; Behr & Helversen, 2004; Fischer et al., 2004; Charlton et al., 2007; Vannoni & McElligott, 2008; Koren & Geffen, 2009). The present study was not designed to reveal the nature of song differences, or to show a correlation between song features and male attributes. However, it suggests that a blue whale song has the potential to convey multiple messages about the sender, such as location and individual identity, at different levels of its temporal and acoustic

structure ('multiple messages hypothesis'; Moller & Pomiankowski, 1993; Johnstone, 1997). This could allow senders to advertise themselves and receivers to assess and potentially identify individual males. Furthermore, encoding individual information in multiple components in conjunction with high redundancy and repetition, increases the ability of receivers to distinguish and potentially discriminate between singers in a spatial dynamic and variable environment. This has also major implications for mate choice. Because asymmetry in parental care often predicts female choice and blue whale males do not appear to defend resources, blue whale songs are likely to represent courtship displays (Andersson, 1994). Consequently, from a female's perspective, the use of multiple cues to identify and extract information on the attributes of the singer may decrease mate-choice errors, particularly when females can listen to several males at once (Candolin, 2003). Furthermore, considering the dispersed nature of blue whales, a female might have to swim huge distances to reach a singer. The costs of mate-choice errors are thus potentially high. Consequently, the use of complex signals might be important in reducing such costs (Candolin, 2003).

In conclusion, this study suggests that, differently to other species with fluid social societies, the main reason why dispersed males are supposed to produce individually distinct songs is for individual assessment in reproduction. This is further supported by the fact that blue whale males do not have easily recognisable social units and do not show obvious cooperative behaviours, even in cases of bigger assemblages in areas of high food abundance (Sears, 2008). However, it is not to exclude that at the same time their songs may also be used by conspecifics to keep track of individual males' locations, for example when travelling between foraging areas, or to coordinate seasonal movements. This is consistent with what has been suggested for another semi-solitary, non-territorial species, the orangutan, where males also produce long-distance calls that primarily function as mating displays, in particular in relation to female attraction (Delgado, 2006; Mitra Setia & van Schaik, 2007).

Whether conspecific blue whales can identify males based on the individual song differences, whether song components convey information on individual's attributes, and females choose mates based on these male cues conveyed in song components remains unknown. Further research is needed to answer these questions and to understand the role and interplay of different individually distinctive traits in the songs of blue whales. It would be important for instance to record the same individual multiple times (e.g. using acoustic tags) during and across seasons. This would help to shed light on the variability or stability of song features over time, which might also be linked to a male's attributes. Furthermore, it would be

interesting to record the same animal at different distances to investigate the attenuation of different song traits, a logistically difficult undertaking with blue whales. Nevertheless, descriptive analyses of signals are useful to set the basis for further more specific investigations, in particular when dealing with animals that are difficult to access and follow such as whales. This study represents a first step towards understanding how blue whales may use differences in the song structure at various levels to distinguish and potentially assess individuals.

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CHAPTER 2

Song divergence in potentially sympatric North Atlantic blue whales

submitted

Song divergence in potentially sympatric North Atlantic blue whales

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ABSTRACT

Geographical variation in acoustic signals can provide insights into the structure and demographics of animal populations. Particularly in zones of sympatry, knowledge of such variation can help to elucidate relationships between populations or conspecific groups, as well as identify the selective forces shaping the variation. North Atlantic blue whales *(Balaenoptera musculus*) are known to roam extensively throughout the ocean basin and travelling males produce intense, redundant, stereotypic songs almost year-round. These songs most likely represent very long-range reproductive displays. Individuals are thus likely to be both acoustically and physically sympatric within the North Atlantic Ocean. Nevertheless, there is controversy about the existence of an eastern and western blue whale population. We studied song variation between eastern and western North Atlantic blue whales. Several song features, including song unit use, unit rate, and the acoustic structure of the predominant unit type showed divergence between the two regions. Furthermore, a multivariate analysis revealed that the frequency parameters in the two North Atlantic regions changed differently over time. Song divergence might be a result of different selective forces acting on distinct features of the structure of blue whale songs. These findings also suggest a subdivision between blue whales in the eastern and western part of the North Atlantic that may represent distinct management units.

INTRODUCTION

Geographical variation in vocalizations has been documented in many vertebrate species and is important for determining the structure and demographics of groups or populations (Mundinger, 1982; Payne & Guinee, 1983; Wilczynski & Ryan, 1999; McGregor et al., 2000; McDonald et al., 2006; Delgado, 2007; Risch et al., 2007; Delarue et al., 2009). Particularly in zones of sympatry, with no interbreeding barriers, investigating the nature of vocal variation between groups of the same species can provide insights into the function and evolution of behavioural differences (Conner, 1982; Mundinger, 1982; Baker & Cunningham, 1985; Grant & Grant, 1996; Weilgart & Whitehead, 1997; Littlejohn, 1999; Hatch & Clark, 2004; Rendell & Whitehead, 2005; Pfennig & Ryan, 2006). Geographical variation between potentially interbreeding populations may result from adaptations to local environmental or ecological conditions (Barrett-Lennard et al., 1996; Slabbekoorn & Smith, 2002b; Dingle et al., 2008), reinforcement of female preferences and male display traits leading to assortative mating (Grant, 1972; Howard, 1993; Littlejohn, 1999; Stewart & MacDougall-Shackleton, 2008), as well as through cultural drift and vocal learning (Slater, 1986; Morrice et al., 1994; Grant & Grant, 1996; Deeke et al., 2000; Van Parijs et al., 2003; Rendell & Whitehead, 2005). Social interactions may also be a strong selective force for the development of sympatric acoustic divergence. Thereby, group-specific vocal traits may evolve to both increase and maintain group affiliation, particularly in species that rely on cooperative behaviours (Ford, 1991; Wilkinson & Wenrick Boughman, 1998; Yurk et al., 2002; Rendell & Whitehead, 2003; Crockford et al., 2004).

Different factors affecting vocal variation may occur simultaneously and are often coupled. For example, song dialects evolve through social learning, and females may prefer to mate with males with local or familiar dialects in order to obtain locally adaptive alleles (Olofsson & Servedio, 2008; Stewart & MacDougall-Shackleton, 2008). Particularly in multicomponent displays such as songs, multiple selective forces may also act on different song traits. Divergence in acoustic reproductive displays between potentially interbreeding populations of the same species has been mainly studied in birds (e.g. Mundinger, 1982; Grant & Grant, 1996; Olofsson & Servedio, 2008) amphibians and insects (e.g., Loftus-Hills & Littlejohn, 1992; Higgins & Waugaman, 2004; Jang & Gerhardt, 2006; Pfennig & Ryan, 2006) but rarely in mammals (Morrice et al., 1994; Van Parijs et al., 2003; Hatch & Clark, 2004).

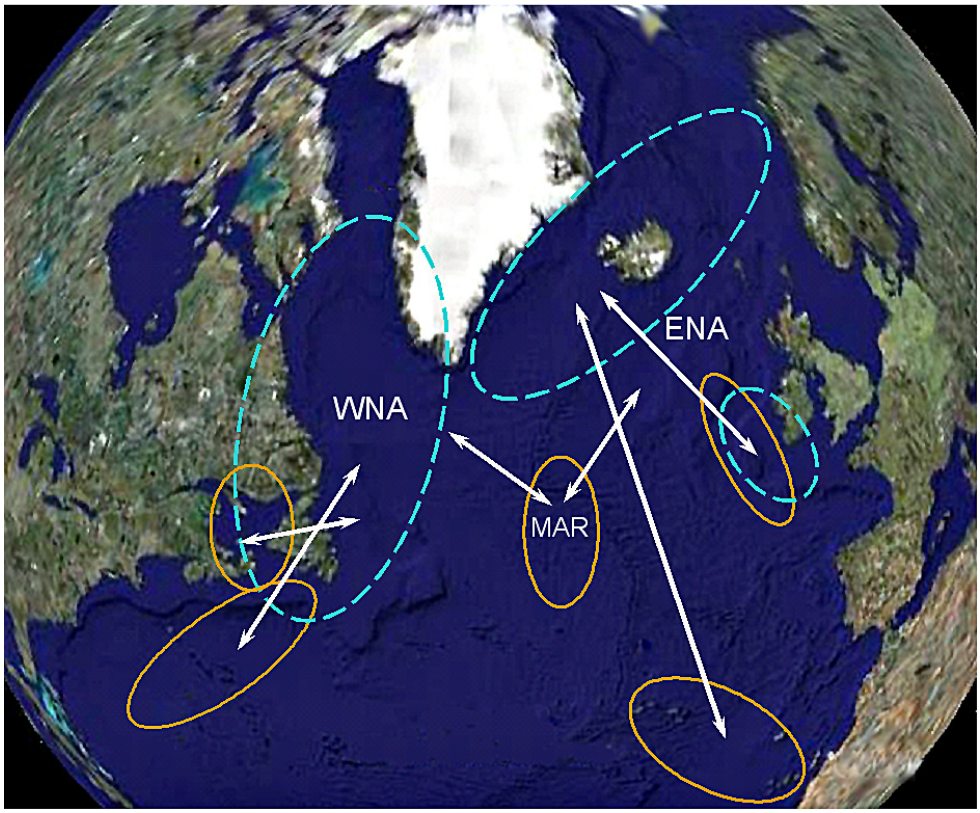

Fig. 1 Map of the North Atlantic showing putative blue whale summer (solid orange ellipse) and winter (dashed blue ellipse) distributions in the western (SL-WNA) and eastern (ENA) North Atlantic. The map was built using combined data reported in the literature from strandings, sightings and acoustic detections (Sigurjònsson & Gunnlaugsson, 1990; Clark, 1995; Reeves & Clapham, 1998; Charif & Clark, 2000; Sears & Calambokidis, 2002; Sears & Larsen, 2002; Mellinger & Clark, 2003; Clark & Gagnon, 2004; Nieukirk et al., 2004; Sears et al., 2005). The arrows indicate potential seasonal movements between the different regions. MAR = Mid-Atlantic Ridge. Size of an ellipse does not indicate animal density.

North Atlantic blue whales are of particular interest with respect to the study of geographical song divergence. Blue whales produce intense, patterned sequences of infrasonic sounds almost year-round (Cummings & Thompson, 1971). These 'songs' are emitted by travelling males and most likely represent long-range reproductive displays (Tyack & Clark, 2000; Oleson et al., 2007). Acoustic tracking of individual blue whales for as much as 40 consecutive days revealed that they can roam extensively (up to several thousands of kilometres) throughout the North Atlantic Ocean and their songs can be heard at ranges of at least many hundreds of kilometres (Clark, 1995; Clark & Gagnon, 2004). The audience can therefore be very vast and due to the movements of individuals with respect to each other, individuals from different regions within the North Atlantic have the potential to be acoustically and/or physically sympatric. This basin-wide roaming has also lead to the

speculation that North Atlantic blue whales are panmictic within an environment that appears to offer no natural boundaries for reproduction. However, little is known about the migration patterns and winter distributions of blue whales inhabiting this ocean basin. Furthermore, there is controversy regarding the existence of an eastern and western population (Donovan, 1991; Sears & Calambokidis, 2002). It also remains unclear whether individuals from the two different regions intermingle and meet elsewhere once leaving the known summer foraging grounds, particularly during the winter, when most reproductive activity is supposed to take place (Fig. 1) (Reeves & Clapham, 1998). Song differences may therefore evince variations in behavioural and social patterns relevant to understanding population structure. Furthermore, investigating geographical differences in blue whale songs has been proven useful and of fundamental importance in defining potential populations or "stocks" (Taylor, 1999; IWC, 2002), and in describing their movements (Charif & Clark, 2000; Stafford et al., 2001; Moore et al., 2002; Mellinger & Barlow, 2003; Stafford et al., 2004; McDonald et al., 2006). This information is thus relevant for management and conservation, especially with regard to endangered and elusive species such as the blue whale.

We investigated whether there were differences in the features and structure of blue whale songs from the eastern and western North Atlantic. Since blue whale songs are multicomponent signals, in which each trait is likely subject to variation, we examined multiple song traits. If we assume that North Atlantic blue whales belong to one population, where all individuals can move, be heard and breed throughout the ocean basin, then songs should not vary substantially. However, if acoustic variation is apparent, then different selective forces might have shaped the blue whale songs of the two North Atlantic regions.

METHODS

Acoustic Recordings and Data Processing

We obtained blue whale recordings from two distinct geographical regions within the North Atlantic: the St. Lawrence Estuary, Qc. Canada, a section of the Western North Atlantic (SL-WNA) and west of the British Isles in the Eastern North Atlantic (ENA). Acoustic data from the SL-WNA were collected from September to October 2003, July to October 2004 and 2005, and October 2005 to July 2006, while those from the ENA were collected between August and February 2000 to 2006 (Table 1).

Table 1 Individual song parameters used in the model and the assignment-test including mean values of the acoustic variables of monotonic units used in the DFA (n = 10 per individual) as well as number of different song unit types used in 1h of each song (only model songs of sufficient length).

Individual	Region	Date	DFA	Dur (s)	T_{rise} (s)	F_{Cmax} (Hz)	F_0 (Hz)	Nr units / 1h song *Hybrid*	*Monotonic*	*Downsweep*	*9-Hz*
1	SL-WNA	9 Oct 2003	model	17.19	8.64	17.92	17.82	5	55	33	1
2	SL-WNA	24 Aug 2004	model	17.70	9.22	17.94	17.84	5	36	17	10
3	SL-WNA	4 Sep 2004	model	17.12	10.59	17.80	17.69	-	-	-	-
4	SL-WNA	8 Sep 2004	model	17.70	12.25	17.79	17.66	7	60	4	21
5	SL-WNA	5 Oct 2004	model	18.00	8.58	17.81	17.68	13	66	5	11
6	SL-WNA	4 Sep 2005	model	21.02	10.54	17.74	17.62	3	46	0	21
7	SL-WNA	9 Sep 2005	model	17.72	9.67	17.91	17.78	0	42	1	11
8	SL-WNA	10 Sep2005	model	17.67	9.94	17.89	17.74	1	73	9	5
9	SL-WNA	15 Sep 2005	model	20.77	10.43	17.72	17.57	0	47	0	15
1	ENA	6 Nov 2004	model	19.30	10.72	17.76	17.63	0	40	0	0
2	ENA	8 Dec 2004	model	15.68	7.66	17.65	17.45	0	24	2	0
3	ENA	25 Sep 2005	model	17.33	7.46	17.75	17.55	0	43	0	0
4	ENA	16 Aug 2006	model	16.33	8.80	17.83	17.67	2	40	0	3
5	ENA	7 Sep 2006	model	19.56	10.15	17.58	17.41	2	40	0	4
6	ENA	11 Sep 2006	model	13.27	7.63	17.62	17.50	0	33	0	0
7	ENA	13 Sep 2006	model	15.69	8.69	17.79	17.66	6	42	0	1
8	ENA	16 Sep 2006	model	16.93	8.73	17.76	17.62	10	30	0	6
9	ENA	21 Sep 2006	model	17.07	8.09	17.63	17.43	-	-	-	-
1	SL-WNA	21 Aug 2004	test	17.47	9.34	18.00	17.83	-	-	-	-
2	SL-WNA	23 Oct 2005	test	17.48	10.25	17.67	17.55	-	-	-	-
3	SL-WNA	4 Dec 2005	test	17.08	8.38	17.72	17.61	-	-	-	-
4	SL-WNA	20 Dec 2005	test	19.14	10.06	17.69	17.56	-	-	-	-
5	SL-WNA	27 Dec 2005	test	18.01	9.41	17.71	17.56	-	-	-	-
1	ENA	25 Nov 2000	test	14.92	9.06	18.24	18.10	-	-	-	-
2	ENA	30 Nov 2000	test	14.87	9.05	17.99	17.92	-	-	-	-
3	ENA	5 Feb 2001	test	14.96	8.78	17.99	17.86	-	-	-	-
4	ENA	6 Feb 2001	test	15.14	9.27	18.00	17.86	-	-	-	-
5	ENA	27 Jan 2006	test	16.50	9.35	17.60	17.43	-	-	-	-

Individuals in bold are those producing songs with monotonic-downsweep pairs (MDP). Abbreviations: St. Lawrence, Western North Atlantic (SL-WNA), Eastern North Atlantic (ENA), duration (Dur), rise time (T_{rise}), maximum contour frequency (F_{Cmax}), fundamental frequency (F_0), discriminant function analysis (DFA). Missing values indicated by dashes.

In the SL-WNA, recordings were made using an array of autonomous bottom-moored recording units referred to as “pop-ups” (Cornell University, Bioacoustics Research Program (CUBRP), Ithaca, NY, USA) (Clark et al., 2002; Clark & Clapham, 2004). In 2003 we used three pop-ups that recorded continuously at a sampling rate of 2kHz. In 2004 and 2005, we deployed five units that recorded continuously at 1kHz. One long-term pop-up (October 2005 – July 2006) was programmed to record at 1kHz with a 50% duty cycle (1h on, 1h off) and to

stop the data acquisition from 1 February to 31 March 2007. This temporary shut down was necessary to prolong battery life until retrieval in summer and enable recordings from April to June, a period in which blue whale sightings have been regularly reported in the area (Ramp et al., 2006). Prior to deployment, we synchronised the units at GPS time (GMT-05:00) to allow correction of clock drift in the system as well as precise synchronisation of multiple units in an array. The units were placed 1.5 - 2 km apart in a triangular or "W"-pattern, depending on their number, at depths between 60 and 100m. Throughout the season, during the periods with no animal sightings, we collected GPS positions of known sound sources (e.g., light bulb breaks), which were used to both validate and calibrate the location accuracy and precision of the array. We calculated locations of singing whales from the arrival-time-differences of their calls as recorded on different recording units in the array. We used an extension of XBAT version 6.1.0.1, a specialised acoustic analysis program written in MATLAB (version 7.0.4, release 13, The Mathworks, Natick, Massachusetts, USA) developed by the CUBRP (Figueroa & Robbins, 2008, www.xbat.org) to calculate the locations of the acoustic source.

In the ENA, we used recordings collected from the U.S. Navy's SOSUS (Sound Surveillance System) that consists of an array of bottom-mounted, fixed hydrophones (Watkins et al., 2000; Clark & Gagnon, 2004). The sounds were recorded at a sampling rate of 1kHz following methods described in Clark and Gagnon (2004) and Mellinger and Clark (2003).

Identification of Individual Song Sequences

When investigating geographical variation it is important to record vocalisations of different individuals in order to prevent sampling bias through over-representation of a few individuals. In the SL-WNA, recordings were collected simultaneously with visual observations during boat surveys (7m rigid-hulled inflatable boat). At each visual encounter with blue whales in the pop-up recording area, we noted the number of whales, the time, and the position of each animal at each surfacing after a dive. At the same time, we used a focal sampling procedure for individual whales to record the GPS position of the individual's dive (seen as a distinctive swirl at the ocean surface in the place where the whale dived) and to take photos of the animal's body coloration pattern and markings for later confirmation of the individual whale's identity. When possible, we conducted focal observations of all animals (usually between 1 and 6) within visual range of the boat in the recording area. These observations lasted so long as to either include three to five surfacing periods, defined as blow cycles, or at least 30min

when whales were feeding at the surface. This procedure enabled us to match the GPS track of an individual at the surface with its acoustic track (if singing) when it was below the surface. This procedure was applied to ensure that the identities of the individuals included in the analysis were known, and no individual was included twice. Six of the nine songs used in the analysis were obtained using this method. However, because position-matching was not always possible, we used a second method to increase the sample size. Even if we were not always able to follow the singer when it was at the surface (i. e., the focal surface animal was not the singer), we attempted to get photo-ids of all animals present during an observation day. This resulted in three additional song samples on three different survey days, when none of the whales visually identified by the first method was encountered (photographic comparison), and on which distinct animals were present (i.e., three days with different "sets" of blue whales).

From the ENA, no surface observations and therefore no GPS-based positions were available. Individual singers were acoustically positioned by cross-fixing bearings to the singer from multiple hydrophone arrays and tracked for at least 28h using identical procedures applied by Clark (1995) and Clark and Gagnon (2004). This method has proven to be effective for following and recording the songs of individual singers for many days. In all cases included here there was no ambiguity as to who produced the song because only days with a single singer were included. This method of recording individuals does not assure that singers from different years are not the same animal. However, because two third of the recordings used for the model (see Statistical Analysis) were obtained from the same year and singers were moving out of the area, we believe that it is highly unlikely that any individual contributed more than once to the song sample.

Song Structure Analyses

We decimated the all recordings from the SL-WNA to a sampling rate of 1kHz to allow a direct comparison between all data from the two study regions. Acoustic data were visualised as continuous 24h-spectrograms using XBAT. Songs were identified using an automatic detector routine in XBAT that selects individual song units based on their template (Brandes et al., 2006). From visual inspections, we chose only sequences for the analysis that had a signal-to-noise ratio sufficient to accurately measure the acoustic variables for all song units (see last paragraph of this section). The units in a song had to feature at least one harmonic, and all the spectral contours of the units had to be distinctive. We used standardised display settings to reduce variation in the accuracy of the frequency and time resolutions.

Spectrograms were calculated by Fast Fourier Transform (FFT size: 2048 points; Hann window; window size: 2.1s with 80% overlap) yielding a temporal resolution of 0.41s and a frequency resolution of 0.24Hz.

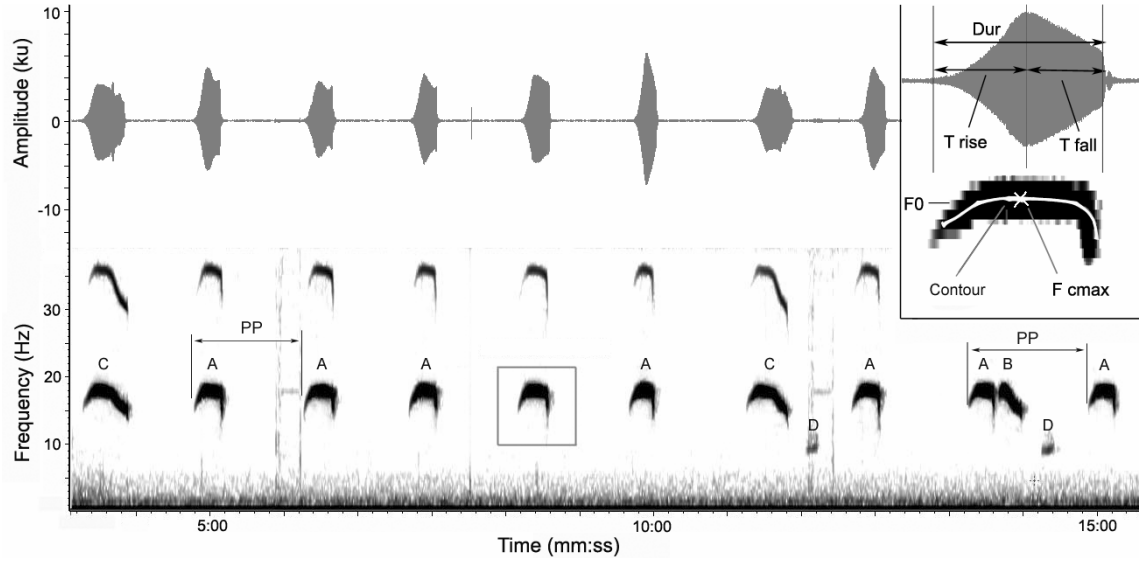

Fig. 2 Waveform and spectrogram of a portion of a typical North Atlantic blue whale song indicating the monotonic unit type used for the comparison (top right). This song contains all four unit types that occur in the North Atlantic: monotonic (A), downsweep (B), hybrid (C) and 9-Hz (D) unit. The monotonic-downsweep pair (MDP) is indicated with AB. Two examples of phrase period are indicated with PP. The recording was made in the SL-WNA (August 24th, 2004). Monotonic call type magnification showing the frequency contour (white line) and the six measured variables: duration (Dur), rise time (T_{rise}), fall time (T_{fall}) measured from the waveform, fundamental frequency (F_0), maximum contour frequency (F_{Cmax}, cross).

Song Unit Use

Blue whale song in the North Atlantic are composed of four different infrasonic sound types, referred to as the (1) monotonic, (2) downsweep, (3) hybrid, and (4) 9-Hz units (Mellinger & Clark, 2003; Nieukirk et al., 2004; Berchok et al., 2006). Units are combined into phrases which are repeated to form a song (described in Mellinger & Clark 2003). There appears to be a high level of stereotypy in the order in which units are produced within a phrase, although not all the unit types are present in all songs (Mellinger & Clark 2003). Monotonic units are the predominant type occurring in every song, which is the reason why we focused on this type of unit. The downsweep unit typically follows a monotonic unit after a short gap of silence and the hybrid unit can be considered a monotonic unit combined with a downsweep unit (Berchok et al. 2006) and often occurs at the beginning of a phrase. The 9-Hz unit often follows hybrid units but can also occur after monotonic or downsweep units (Di Iorio, unpublished data). We easily recognised and identified unit types by visual inspection of

spectrograms (Fig. 2) and counted the number of each unit type in the first hour of each individual song. For a better visualisation of song unit use, we also determined the proportions (expressed as percentages) of unit type occurrence in 1h of each song. The 1h song metric was only used for this analysis.

Temporal Pattern

We measured time intervals between monotonic units and rates of production of song units for the songs from the two geographical regions. Unit intervals were calculated as the absolute difference between the begin time of one monotonic unit and the begin time of the next monotonic unit, called *phrase period* (PP) (Mellinger & Clark, 2003; Fig. 2). We only considered PPs within a sequence excluding the long intervals of silence between unit sequences that likely correspond to the whale's respiration breaks (Mellinger & Clark, 2003). To compare *unit rates* between the songs of the two regions, we divided each individual's song into 5-minute samples and counted the number of units of all the different types within each sample, so by this procedure unit rates are in units/5-minute sample. We randomly chose eight 5-minute windows per song.

Acoustic Structure

We measured the spectral and temporal variables on 10 randomly chosen monotonic units per individual song. We chose only monotonic units that were not immediately followed by a downsweep unit because we wanted to reduce the possible influence of unit sequence in the analysis (Fig. 2). We measured two spectral parameters and three temporal parameters from all the selected monotonic units. The two spectral parameters were fundamental frequency (F_0) and maximum contour frequency (F_{Cmax}). We calculated F0 as the average of the values of the fundamental frequency along the contour of the centre part of the unit (at 80 different points) and F_{Cmax} was the maximum frequency along this contour (Fig. 2). We did not measure start and end frequency because they are lower in amplitude than the centre of the unit and potential differences might be attributed to different recording distances and not geographical regions (Berchok et al., 2006). Aforementioned variables were measured using the frequency contour measurement extension in XBAT (Cortopassi, 2004). The three temporal parameters were unit duration (Dur), rise time (T_{rise}) and fall time (T_{fall}). These were measured from the waveform in Raven Pro (version 1.3. CBRP, Ithaca, NY) (Fig.2).

Statistical Analysis

For all but two geographical comparisons we used nine high-quality, songs of nine individuals from each of the two geographical regions. These songs were all recorded during similar times of the year (model songs) (Table 1). Because two individuals, one from each geographical region, produced short songs, approx. 30min each, they were excluded form the unit use and the temporal pattern analysis. Therefore, only eight out of the nine songs per region were used for the analysis of song unit use, PP and unit rate (songs omitted: SL-WNA: 4 Sept 2004, ENA: 21 Sept 2006) (Table 1).

Song Unit Use

Geographical variation in *song unit use* was tested by conducting four non-parametric Mann-Whitney-U tests, one for each unit type. The tests were conducted with the number of units present in 1h of song.

Temporal Pattern

To investigate the regional effect on *PP* (PP: 670, 42±15 per individual, N=16), we used a general linear mixed effects model (LMM) procedure fitted with residual maximum likelihood estimation (REML, lme function) (Venables & Ripley, 2002). Individuals were fitted as random term to control for repeated measurements, Regions and Year (to control for a time effect) including interactions were fitted as fixed effects. Furthermore, since SL-WNA whales sang more songs containing regular monotonic and downsweep unit pairs (MDP) than ENA whales (Fig. 2), which could influence the outcome of the PP and unit rate analysis, we also added 'Song type' as a fixed factor. Songs containing more than six MDP were classified as 'MDP songs' (Table 1). The same model was also used to test regional effects on *unit rate* (Unitsx5min-samples: 128, 8 samples per individual, N= 16).

Acoustic Structure

To investigate the effect of regions on the acoustic parameters of monotonic units (180 monotonic units, 10 monotonic units per individual, N= 18) and control for a year's effect, we conducted a LMM for all acoustic parameters with Regions and Year (including interaction) as fixed factors and Individuals as random factor. All the statistical analysis up to here were performed using R (version 2.7.1., R Development Core Team 2006).

Acoustic variables that were shown to best distinguish geographical regions, were used in a cross-validated discriminant function analysis (DFA) with geographical region as the grouping variable. Because the DFA only permits the consideration of a single factor at the time, using multiple replicates per individual would have resulted in pseudoreplication (Mundry & Sommer, 2008). Therefore, we used mean values per individual for each monotonic unit variable. DFA is useful for building a predictive model of group membership based on observed characteristics, and it allows estimation of the parameters that contribute most to group separation (Tabachnick & Fidell, 2001). The DFA derives one (or multiple) discriminant function(s), representing a linear combination of the variables (predictor variables) that best assigns individuals (cases) into their correct geographical region (pre-determined group). The classification error was assessed using the leave-one-out cross-validation, where one case is left out of the training set and then used as a test set. This process was repeated for all the cases in the data set, which is particularly appropriate when sample sizes are small, yielding an estimate of the accuracy of the method (Lachenbruch & Mickey, 1968; Goutte, 1997; McGarigal et al., 2000).

Assignment-test

If the classification score of the predictive model of group membership built by DFA is high, then DFA also allows assignment of novel cases to a predetermined group using the discriminant function generated from the model cases. In order to evaluate how effective the DFA model was at correctly assigning non-model data to the respective geographical region, we selected novel, previously unassigned, test songs recorded in different years (2000-2006) and different seasons, and used the same acoustic variables measured for model songs as input to the DFA model. We used ten high-quality song sequences: five from the SL-WNA and five from the ENA (Table 1). We processed the song sequences, selected the monotonic units, and measured the acoustic variables as described above for the model songs. DFA for model and assignment-test data was computed using SPSS (for Windows, version 16.0, SPSS Inc., Chicago USA).

RESULTS

Song Unit Use

Blue whale songs from eastern and western North Atlantic regions did not differ in the types of units from which songs are composed, but they did differ in the occurrence of each unit

type. SL-WNA singers produced generally more of each unit type than ENA singers (Table 2). The greatest difference was observed in the use of the 9-Hz unit (Mann-Whitney U: N = 16, U = 4.5, P < 0.001) followed by the downsweep (Mann-Whitney U: N = 16, U = 11.0, P = 0.004) and the monotonic unit (Mann-Whitney U: N = 16, U = 15.5, P = 0.027). Hybrid unit occurrence did not differ between regions (Mann-Whitney U: N = 16, U = 32.5, P = 0.471). Furthermore, table 2 indicates that the proportion of monotonic units is much higher in ENA than WNA songs and that in the WNA, whales produced more diverse songs, using more types of units, than in the ENA.

Table 2. Summary of counts and percentages of unit type occurrence per geographical region (western North Atlantic, SL-WNA, and eastern North Atlantic, ENA) measured from 1h of each of the model songs (N=16). Percentages indicate the proportion of each unit type in relation to the total number of units within a region (within Region) and to the total number of units for the two regions combined (% of total).

			Unit type				Total
			Hybrid	Monotonic	Downsweep	9-Hz	
Region	ENA	Count	20	292	2	14	328
		% within Region	6.1%	89.0%	0.60%	4.3%	100.0%
		% of Total	2.1%	30.7%	0.20%	1.5%	34.5%
	SL-WNA	Count	34	425	69	95	623
		% within Region	5.5%	68.2%	11.10%	15.2%	100.0%
		% of Total	3.6%	44.7%	7.30%	10.0%	65.5%
Total		Count	71	54	717	71	951
		% of Total	7.5%	75.4%	5.7%	7.50%	100.0%

Temporal Pattern

PPs did not show significant geographical differences, it was not affected by years and the two types of songs did not differ in PP (LMM: $PP_{Regions}$, $F_{1, 11} = 0.19$, P = 0.67 ; PP_{Year} , $F_{1, 11} = 0.05$, P = 0.82; $PP_{Regions*Year}$, $F_{1, 11} = 0.03$, P = 0.87 ; $PP_{SongType}$, $F_{1, 11} = 3.29$, P = 0.10, N=16). *Unit rate* showed highly significant regional variation, with SL-WNA rates being higher than the ENA ones (Fig. 4, Model), but no effect was observed neither for recording year nor song type (LMM: $UnitRate_{Regions}$, $F_{1, 11} = 37.91$, P = 0.001; $UnitRate_{Year}$, $F_{1, 10} = 0.92$, P = 0.36; $UnitRate_{Regions*Year}$, $F_{1, 11} = 2.27$, P = 0.16; $UnitRate_{SongType}$, $F_{1, 11} = 0.61$, P = 0.45, N=16). (Table 3).

Acoustic Structure

Based on the 18 model individuals, there were highly significant regional but no recording year differences in the spectral parameters F_0 (LMM: $F_{0\ (Regions)}$, $F_{1,\ 14}$ = 12.3, P = 0.004; $F_{0\ (Year)}$, $F_{1,\ 14}$ = 0.2, P = 0.68; $F_{0\ (Regions*Year)}$, $F_{1,\ 14}$ = 0.8, P = 0.4) and F_{Cmax} (LMM: $F_{Cmax\ (Regions)}$, $F_{1,\ 14}$ = 11.0, P = 0.005; $F_{Cmax\ (Year)}$, $F_{1,\ 14}$ = 1.53, P = 0.24; $F_{Cmax\ (Regions*Year)}$, $F_{1,\ 14}$ = 1.06, P = 0.32) (Fig. 4) as well as in the temporal parameter T_{rise} (LMM: $T_{rise\ (Regions)}$, $F_{1,\ 14}$ = 5.46, P = 0.03; $T_{rise\ (Year)}$, $F_{1,\ 14}$ = 0.02, P = 0.89; $T_{rise\ (Regions*Year)}$, $F_{1,\ 14}$ = 0.19, P = 0.67). Duration showed a moderate geographical but no recording year effect (LMM: $Dur_{(Regions)}$, $F_{1,\ 14}$ = 3.78, P = 0.07; $Dur_{(Regions)}$, $F_{1,\ 14}$ = 0.02, P = 0.09; $Dur_{(Regions*Year)}$, $F_{1,\ 14}$ = 3.09, P = 0.10). The values of all these variables were greater in the SL-WNA than in the ENA (Fig. 3, Model years). No significant geographical nor recording year differences were found for T_{fall} (LMM: $T_{fall\ (Regions)}$, $F_{1,\ 14}$ = 0.05, P = 0.82; $T_{fall\ (Year)}$, $F_{1,\ 14}$ = 0.06, P = 0.81; $T_{fall\ (Regions*Year)}$, $F_{1,\ 14}$ = 2.63, P = 0.13) (Table 3, Fig. 3).

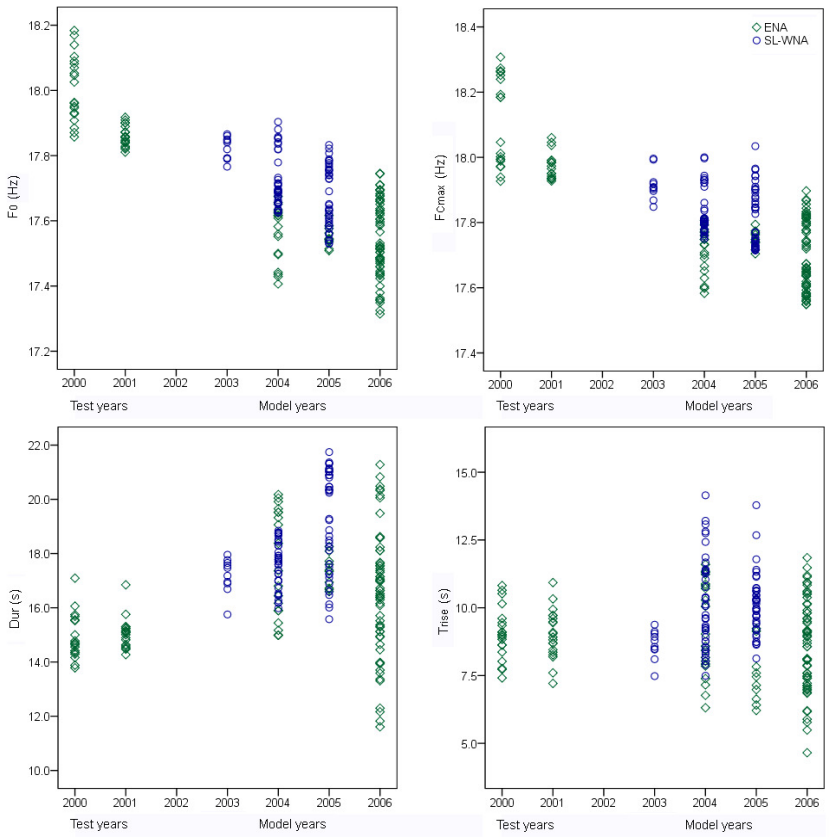

Fig. 3 Distribution of frequency and temporal variables between monotonic units of songs from the eastern (ENA) (green) and western North Atlantic (SL-WNA) (blue). Single values of 10 units per individual song are shown. The figure illustrates divergence of the fundamental frequency (F_0), the maximum contour frequency (F_{Cmax}), the duration (Dur), and the rise time (T_{rise}) between model songs (N=9 per region) recorded between 2003 (one song) and 2006 (Model years) and also with respect to values form the ENA test sequences recorded in 2000 and 2001 (N=4, Test years).

Table 3 Means and standard deviation (SD) for all measured acoustic variables of the monotonic units, phrase periods (PP), and unit rates per geographical region (SL-WNA and ENA). Acoustic variable measurements are subdivided between model and assignment-test songs and between years within the ENA test songs (old: ENA 2000/01, recent : ENA 2006).

Acoustic variables			**N**	**Mean**	**SD**
Dur (s)	**Model**	SL-WNA	9	18.32	1.619
		ENA	9	16.80	2.15
	Test	SL-WNA	5	17.84	0.97
		ENA 2000/01	4	14.97	0.70
		ENA 2006	1	16.50	1.31
T_{rise} (s)	**Model***	SL-WNA	9	10.01*	1.43
		ENA	9	8.63	1.67
	Test	SL-WNA	5	9.49	1.10
		ENA 2000/01	4	9.04	0.92
		ENA 2006	1	9.35	1.86
T_{fall} (s)	**Model**	SL-WNA	9	8.31	1.86
		ENA	9	8.15	1.70
	Test	SL-WNA	5	8.34	1.05
		ENA 2000/01	4	5.94	0.96
		ENA 2006	1	7.15	1.15
F_{Cmax} (Hz)	**Model***	SL-WNA	9	17.84	0.08
		ENA	9	17.71	0.09
	Test	SL-WNA	5	17.75	0.13
		ENA 2000/01	4	18.06	0.14
		ENA 2006	1	17.60	0.08
F_0 (Hz)	**Model***	SL-WNA	9	17.71	0.09
		ENA	9	17.55	0.11
	Test	SL-WNA	5	17.62	0.11
		ENA 2000/01	4	17.94	0.11
		ENA 2006	1	17.43	0.06
Temporal Pattern					
PP (s)	**Model**	SL-WNA	8	72.61	3.56
		ENA	8	73.72	2.46
Unit rate (Nr/5min)	**Model***	SL-WNA	8	6.48	0.69
		ENA	8	4.91	0.10
	no MDP*	SL-WNA	6	6.40	0.53
		ENA	6	4.92	0.31

N indicating number of individual songs; no MDP indicating songs without monotonic-downsweep pairs. * indicates significant differences between the model songs of the two regions, $P < 0.05$, in the LMMs.

The DFA using the individual mean values of F_0, F_{Cmax}, T_{rise}, and Dur revealed acoustic differentiation between the two regions (Wilk's lambda = 0.365, $X^2 = 14.123$, P = 0.007). Cross-validated DFA correctly classified 16 out of 18 (88.9%) individuals (Table 4). The classification of previously unassigned individuals in the assignment-test resulted in five

misclassifications for the 10 test songs. Four misclassified units were from ENA songs recorded in 2000 or 2001 (Table 4). All frequency values of the units recorded from 2000 and 2001 were higher than those from song units recorded in 2004, 2005, and 2006 used for the model as well as for the correctly classified song recorded in winter 2006 (Table 1, Fig. 3). One misclassification was from the SL-WNA and was recorded on 27 Dec 2005.

Table 4. Classification results for the geographical comparison (model) and the assignment-test. The geographical comparison computed using 18 known individuals resulted in two misclassifications, one for each geographical region (bold number in Model section). For the assignment-test, 4 songs from the ENA (all deriving from recordings made in 2000 and 2001) and one from the SL-WNA were misclassified (bold number in assignment-test section).

				Predicted Group Membership		
			Region	SL-WNA	ENA	Total
Model	Cross-validated	Count	SL-WNA	8	**1**	9
			ENA	**1**	8	9
Assignment-test		Count	SL-WNA	4	**1**	5
			ENA	**4**	1	5

DISCUSSION

We studied geographical variation in the songs of eastern (ENA) and western (SL-WNA) North Atlantic blue whales that have the potential to be acoustically and/or physically sympatric. We found that blue whales from the two regions showed variation in the use of song unit types, unit rate as well as in the acoustic features of the most common unit type, the monotonic unit. A DFA model based on variables from individual songs recorded within the same time period in late summer/autumn between 2004 and 2006 in the two regions, correctly classified 88.9% of the individual songs, indicating a clear distinction between the two geographical regions in the structure of monotonic units. However, the discriminating ability seemed to be constrained by time. Older ENA songs from 2000 and 2001 were all misclassified as SL-WNA songs. The reason for these misclassifications appears to be a result of changes in the songs' frequency characteristics measured as an overall downward shift in fundamental frequency (F_0) and maximum contour frequency (F_{Cmax}) in ENA songs (Fig. 3). However, it is not clear whether and to which extent this downward shift in frequency also occurred in blue whale songs of the SL-WNA due to a lack of older recordings in this region.

Yet, a previous study on blue whale songs recorded in the same area of the SL-WNA during a similar time period as older ENA songs (1998-2001) reported mean maximum frequencies of 18.6Hz (Berchok et al., 2006). Furthermore, Mellinger and Clark (2003) described blue whale songs throughout the western North Atlantic from 1993 to 1994 with monotonic unit fundamental frequencies between 18.3 and 18.5Hz, and Edds (1981) reported fundamental frequencies of 19.4Hz in 1979. This indicates that the values observed in the ENA in 2000 and 2001 are similar or slightly lower than those found in the WNA in similar years (Table 3). Consequently, a decrease in frequency parameters occurred in both regions of the North Atlantic but over the same time period, ENA blue whales decreased the overall frequency content of their song units consistently more than SL-WNA whales did (Fig. 3).

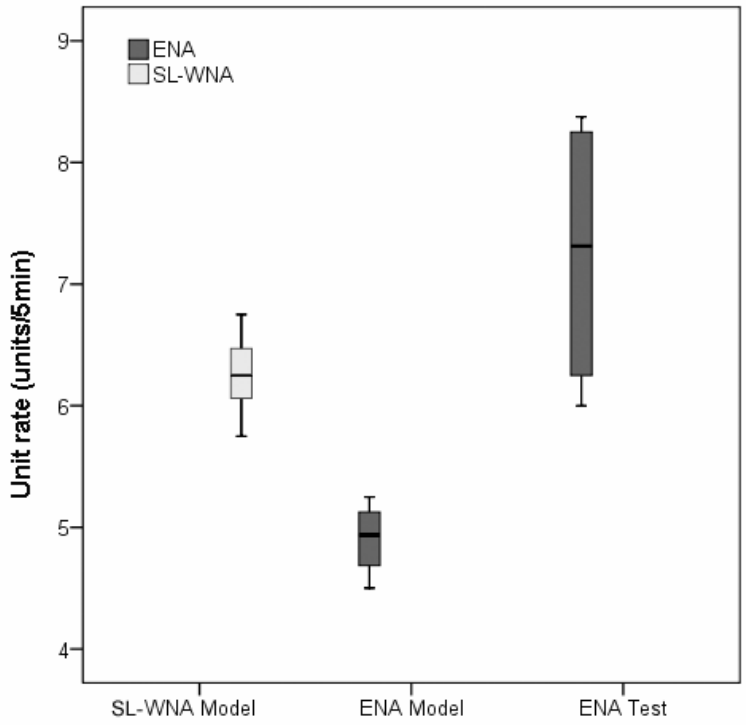

Fig. 4 Differences in unit rate (nr units per 5min) between songs form the eastern and western North Atlantic. Mean value and standard deviations are shown. The figure illustrates differences between model songs recorded from 2003-2005 in the WNA and 2004-2006 in the ENA (N=8 per region, ENA Model, SL-WNA Model), and also relative to ENA test sequences recorded in 2000-2001 (N=4, ENA Test).

Geographical differences were also observed in the unit rates, with SL-WNA blue whales producing more units per time interval than ENA whales. This variation might be linked to the observed shift in frequency parameters in the ENA. The production of lower-

frequency song units might be energetically compensated with a reduction of unit rate (Wilczynski & Ryan, 1999). Indicative for this hypothesis is the fact that older ENA songs with an overall higher frequency, also showed a higher unit rate (Fig. 4). Higher unit rates could also be linked to higher fitness or better quality of singing males (McComb, 1991; McElligott et al., 1999; Gerhardt & Huber, 2002; Kitchen et al., 2003; Craul et al., 2004). However, data on fitness differences are not available for the blue whales of the two North Atlantic regions and are also methodologically very difficult to obtain.

North Atlantic blue whales did not differ with respect to the types of units from which a song is composed (see also Mellinger & Clark 2003, Berchok et al., 2006) but did differ in the use of different unit types. Blue whale songs throughout the North Atlantic are composed of four unit types, the monotonic, the downsweep, the hybrid, and the 9-Hz unit. SL-WNA blue whales emitted more of each type, but the biggest difference was in the production of 9-Hz, downsweep, and monotonic units. Furthermore, SL-WNA whales not only produced more of each unit type but their songs were also more diverse, using proportionally more of each type of unit compared to their conspecifics in the ENA. The higher occurrence of the different unit types in the SL-WNA might be linked to the higher unit rate, because the more units are produced per time interval the higher their proportion within a song. The higher presence of downsweep units in the SL-WNA might be related to the fact that blue whales of this region produced more songs containing monotonic-downsweep pairs than ENA whales. Moreover, the predominant difference observed in the production of 9-Hz units could also be related to the fact that this song component is produced at relatively lower intensity levels than monotonic units (ca. 20-30dB, representing the relative received level value between monotonic and 9-Hz units; Clark & Di Iorio, unpublished data) and in the ENA the singers were located much farther from the hydrophones (e.g., > 15 miles), so that even if ENA whales produced this unit type they might not always have been detected. However, all recordings were of high quality, showing at least one harmonic with similar received levels as 9-Hz units (Di Iorio, unpublished data), thus weakening this explanation. To correctly explore the relationships between song composition at the unit level and geographical origin in blue whales, studies should be conducted with a larger sample of songs, and including repeated recordings of the same individuals within the same season, and from different seasons and years. This would provide a measure of temporal stability within individuals and regions, but it is also a rather daunting undertaking considering the dispersed nature of the whales and the difficulties of acquiring multiple song samples from known individuals.

Overall, we found differences at multiple levels in the songs of SL-WNA and ENA blue whales, despite the lack of obvious typological variations at the initiation of this study. A potential factor driving the observed divergence is local adaptation to the environment or ecological niche (e.g., Slabbekoorn & Smith, 2002a; Sugiura et al., 2006; Parks et al., 2007). Particularly the different decrease in the frequency parameters found between the two regions could be attributed to differences in background noise levels. Ship traffic and consequently ambient noise is much higher in the SL-WNA than the ENA. The main frequency band of blue whale songs (10-35Hz) coincides with an acoustic window of low ambient noise (Clark & Ellison, 2003). However, if mean low-frequency ambient noise increases over time, individuals might avoid masking by further decreasing their fundamental frequency. This might account for the general frequency drop observed in both areas, but it is in contrast with our findings showing a more rapid and pronounced decrease in the ENA, which was characterised by a lower level of shipping compared to the WNA. The different rates of change in frequency parameters may be a result of inter-specific competition for acoustic signalling space between ENA blue and fin whales (*Balaenoptera physalus*). The striking difference between the two regions was the heavy presence of fin whales in almost all ENA recordings, visible as a nearly continuous black band between 18 and 22Hz in the spectrogram of sound files of all analysed years (Clark, unpublished data). Fin whales outnumber blue whales, and the potential masking properties of their overlapping songs might have forced the ENA blue whales to lower the frequency of their own song units. The SL-WNA blue whales have not been subject to an elevated presence of singing fin whales in the St. Lawrence Estuary, and thus might not have undertaken a character displacement as did the ENA whales. However, present data were not designed to test these hypothesis, but they provide an important foundation to investigate this issue further.

Since blue whale songs are supposed to be mating displays, sexual selection is likely to influence signal evolution. Female preferences for song traits for example, are known to direct selection on male signals and be further reinforced if linked to fitness benefits (Marshall et al., 2003; Littlejohn, 1999; Stewart & MacDougall-Shackleton, 2008). Many of the observed differences in the structure and features of songs (e.g., unit use, unit rate, frequency) may have resulted from female preferences for specific characteristics or for familiar songs, as shown across taxa (insects and frogs: Wilczynski & Ryan, 1999; Gerhardt & Huber, 2002; Höbel & Gerhardt, 2003; Hunt et al., 2005; birds: Baker et al., 1981; Searcy & Yasukawa, 1996; Gil & Slater, 2000; Drăgănoiu et al., 2002; mammals: McComb, 1991; Davidson & Wilkinson, 2004; Puts, 2005; Behr et al., 2006; Koren & Geffen, 2009). However, our study

was not outlined to reveal these relationships, and no preference tests on blue whale females could be carried out so far.

Social factors might also have been driving the observed geographical variation. In North Atlantic blue whales, if individuals of the two geographical regions are acoustically sympatric, those that produce songs with region-specific features might gain an advantage when travelling over long distances between wintering and summering areas because "group"-cohesion would be enhanced by a decrease of the probability of confusion. Selection might therefore lead to reinforcement of vocal traditions and thus divergence. Group-specific variation in sympatrically living marine mammals has been described for several species and mainly attributed to vocal learning in relation to vocal traditions or to site fidelity (Ford, 1991; Morrice et al., 1994; Yurk et al., 2002; Van Parijs et al., 2003; Rendell & Whitehead, 2005). In sperm (*Physeter macrocephalus*) and killer (*Orcinus orca*) whales for instance, different groups (called clans) show group-specific variation in socially relevant calls, which likely are essential in maintaining group cohesion or in coordinating cooperative behaviours such as foraging or defence (e.g. Barrett- Lennard et al., 1996; Baird, 2000; Rendell & Whitehead, 2003).. These group-specific acoustic traits are culturally transmitted and stable over time (Yurk et al., 2002; Rendell & Whitehead, 2005). Blue whales, do not form stable long-term social units like sperm or killer whales, nor do they show cooperative behaviours (Sears et al., 1990). Song transmission has been shown in a closely related species, the humpback whale (*Megaptera novaeangliae*) (Noad et al., 2000). However, besides one report of a blue whale potentially mimicking a song unit of a different population with a distinct song (Stafford & Moore, 2005), vocal learning has not been shown in this species until now. Although it is not clear what benefits blue whales would derive from within-group convergence of songs, they could still be used to communicate to conspecifics over long distances and maintain a network of loose associations that may be important for inter-individual interactions, as for example for mate attraction.

Another possible reason for the observed geographical variation, is that the two groups simply differ in their songs because individuals are geographically isolated throughout the year to a grater extent than we assumed. North Atlantic blue whales were decimated by commercial whaling, and the estimated population is on the order of several thousand individuals (Clapham & Baker, 2001). Consequently, encounter rates between individuals from the two sides of the ocean basin might have decreased considerably, resulting in a more pronounced spatial separation between the two groups. This spatial separation might now be

reflected as a divergence in song features. As discussed, different factors might have acted simultaneously on different song components. More studies are needed on a) the temporal stability of different song characteristics over time b) female preferences for particular songs features, and c) potential fitness consequences of producing region-specific songs that would help shed light on the forces influencing this geographical variation.

An important issue in considering geographical variation in vocalisations is the likelihood of animals interbreeding over the scales in question (Rendell & Whitehead, 2005). This is of utmost concern if the vocal signals are involved in reproduction. Genetic analysis may thus be useful in determining the level of reproductive isolation between the two groups. However, if the variation is dependent on ecological factors (e.g., acoustic niche competition) or cultural drift, there is potential for substantial gene flow between blue whales of the two regions (Slabbekoorn & Smith, 2002a; Van Parijs et al., 2003; Rendell & Whitehead, 2005). Furthermore, as proposed for North Atlantic fin whales that show strong song variation in zones of sympatry, evidence for genetic divergence can also depend on the onset of acoustic divergence (Hatch & Clark, 2004). If the differences in acoustic signals are only recent, a genetic correlation might not yet be detectable, regardless of the type of selecting force.

In conclusion, our results and photo-ID efforts by others showing a lack of photographic matches between eastern and the western North Atlantic animals (Sears & Calambokidis, 2002) suggest the existence of two North Atlantic groups that might represent distinct stocks, consistent with Gambell (1979). Consequently, these observations indicate a separation between eastern and western North Atlantic blue whales at least during the summer feeding period (when photographs are taken). This distinction between eastern and western North Atlantic blue whales is further supported by the results obtained from the assignment-test, which suggest that blue whales from the two regions might in part be exposed to different selective pressures (i.e., signal interference by fin whales). Furthermore, we have shown that the exploration of even small geographical differences can be used to detect different trends in the vocal development of neighbouring and potentially sympatric individuals or groups. Therefore, also apparently subtle difference can contribute to better understand the evolutionary ecology and structure of a population. These results also show that song feature differences can arise over a period of time that is less than a generation, an indication that certain song characteristics are labile and subject to rapid changes. We therefore suggest that long term-studies are needed to better understand evolutionary processes of geographical variation in acoustic signals, also in the scope of management programs.

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CHAPTER 3

Solitary singers and social introverts?

Evidence for audience and context-dependent use of song units in blue whales

to be submitted

Photo: Petra Reimann

Solitary singers and social introverts?

Evidence for audience and context-dependent use of song units in blue whales

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ABSTRACT

When many senders and receivers share the same signalling space, the social environment of an individual can significantly influence signal output. A signaller might for instance adjust signal emission depending on the audience. Blue whales (*Balaenoptera musculus*) live in a dispersed and very fluid social environment. Males produce long-ranging infrasonic sounds with potential reproductive function, either patterned in long sequences, called 'songs' or singularly in irregular short sequences referred to as 'fragments'. We examined if the production of songs or fragments was differentially affected by factors delineating the social context (e.g., number of animals, number of pairs, or males and females present within a short range), and described the seasonal onset of infrasonic sounds in relation to formation of female-male bonds. We conducted the study during the summer feeding period and found that blue whales started to emit infrasonic sounds at the same time with the formation of female-male bonds. However, song production was not affected by any of the social variables, whereas fragment production depended on the number of females and single whales present within a short range. Furthermore, songs were emitted by travelling individuals, as already reported elsewhere, whereas fragments were produced in situations where multiple animals were congregated and engaged in stationary behaviours (e.g., stationary feeding, social interactions). Combined, our results suggest a link between infrasonic unit production and reproduction in blue whales, but different social and behavioural contexts for the two types of infrasonic sound outputs.

INTRODUCTION

In many species, communication often occurs within a network where several senders and receivers share the same active signalling space (McGregor & Peake, 2000; McGregor, 2005). In addition to seasonal, ecological or behavioural factors, signalling can be affected by the social environment, since the presence of different potential receivers can influence signal output (Catchpole, 1973; Bradbury & Vehrencamp, 1998). Advertisement displays such as songs might be particularly concerned because they are suited for long-range transmission and encompass a large number of individuals (Wiley & Richards, 1982; Naguib & Wiley, 2001). Moreover, songs are sexually selected traits that function either to attract mates or/and to repel rival males, and they usually act at a distance (Catchpole, 1973; Andersson & Iwasa, 1996; Bradbury & Vehrencamp, 1998). Song emission can thus depend on the composition of the audience as well as on the distance of potential receivers. In zebra finches (*Taeniopygia guttata*) for example, the rate of 'undirected songs' (i.e., not directed at any specific receiver) is more depressed by the presence of females rather than males as well as by the close presence of familiar than stranger companions (Dunn & Zann, 1997). Furthermore, in bats, males use distinct categories of song types when engaged in inter-sexual versus intra-sexual communication (sac-winged bat *Saccopteryx bilineata*, Behr & Helversen, 2004). Investigating patterns of variability of song production with respect to the audience can therefore provide insights into the functional significance of different types of song output.

Blue whales (*Balaenoptera musculus*) live in a fluid social network. Individuals are primarily found alone, in pairs or in small unstable groups, although larger assemblages can be observed when they congregate during summer feeding (Clark & Fristrup, 1997; Hucke-Gaete et al., 2004; Sears, 2008). Furthermore, males are non-territorial, they range extensively and emit hierarchically organised, redundant sequences of sounds (songs) almost year-round, which are assumed to be male reproductive displays (Tyack & Clark, 2000, Oleson et al., 2007). In the typical deep sea habitat of blue whales, songs are suited to be transmitted over long distances (Bass & Clark, 2003; Clark & Ellison, 2003). In fact, depending on oceanographic and environmental conditions (e.g., noise, temperature, salinity), blue whale singers can potentially be heard by other individuals at ranges of at least hundreds of kilometres (Payne & Webb, 1971; Clark, 1995; Clark & Ellison, 2003). As a consequence, the potential audience can be very vast. Moreover, songs appear to be emitted only by travelling males out of visual contact with other individuals (Oleson et al., 2007). This implies that the

signaller is not always aware of who is within hearing range, suggesting that song is undirected. Blue whales also emit single or short non-patterned sequences of the same infrasonic sounds composing a song (Oleson et al., 2007). These 'fragments' were described as being produced in various contexts, such as feeding or resting, and where two to three whales were in close association (Oleson et al., 2007). The functional significance of these different types of song unit sequences is not clear.

The aim of this study was to examine the occurrence of songs and fragments within the frame of the social environment in which they are emitted. Summer foraging grounds are particularly interesting in this respect, because animals are thought to be primarily feeding to build up their energy reserves and only marginally engaged in activities linked to reproduction (but see Clark & Clapham, 2004). The importance of the social context in relation to patterns of song units production might therefore be intensified, because unless a male has a potential advantage in advertising himself, he would probably not do it on the expenses of gaining energy through feeding. There is evidence for a conflicting relationship between song production and food consumption in blue whales (Stafford et al., 2005; Oleson et al., 2007). In fact, songs have been described to be mainly emitted during night time, when feeding is thought to be less efficient (Stafford et al., 2005) and never while deep feeding during the day (Oleson et al., 2007). In contrast, fragments also occurred during daytime when animals were feeding (Oleson et al., 2007). The authors suggested that the production of songs and feeding are mutually exclusive and that the differences in the types of song unit output reflect this trade-off between feeding and singing.

In this kind of conflicting circumstances, the role of social factors in the production of song patterns may be fundamental, primarily because if song unit emission is linked to reproductive behaviour, it is most probably affected by the audience (Andersson & Iwasa, 1996). In this study we examined this hypothesis by testing how the social environment (e.g. number and composition of conspecific audience) affected the probability of producing either songs or fragments. Moreover, we also investigated the variation of song unit occurrence during the season, the onset and seasonal occurrence of inter-sexual associations, and the diel trend of the two types of song unit outputs. These explorative analyses described the temporal and contextual frame of song unit production as well as changes in the social environment that might be important in understanding the role of reproductive displays in a feeding context.

METHODS

Study Site and Subjects

We conducted this study in the St. Lawrence Estuary, Qc. Canada (western North Atlantic, 49.5 N, -69.0 E) from July to October 2004 and 2005 as part of a larger project (Di Iorio, 2009). During this period, a portion of the North Atlantic blue whales aggregate in this nutrient-rich waters to feed. In early autumn, in concurrence with the approaching breeding season, both social interactions and the formation of female-male associations are frequently observed (Sears et al., 1990; Berchok et al., 2006). Blue whales can be individually recognised by the pigmentation on their flanks and most of the animals present are listed in a catalogue for the western North Atlantic (Sears et al., 1990). A high proportion of the blue whales observed in the area are frequently re-sighted in subsequent years and the sex ratio is approximately 1:1 (Ramp et al., 2006).

Acoustic Recordings and Locations

Songs of North Atlantic blue whales are composed of four different infrasonic sound types: the (1) monotonic, (2) downsweep, (3) hybrid, and (4) 9-Hz units (Edds, 1982; Mellinger & Clark 2003; Berchok *et al.* 2006) (Fig. 1). Units are combined into phrases which are repeated in a pattern to form a song (Mellinger & Clark 2003).

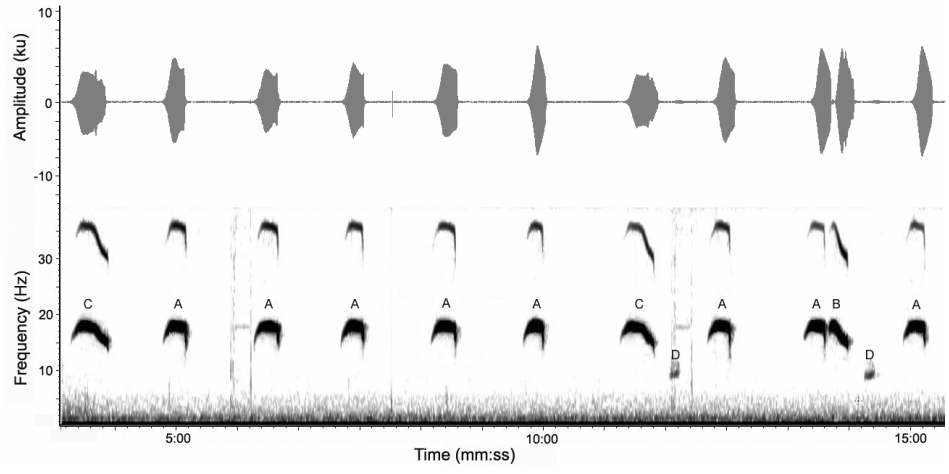

Fig. 1. Waveform and spectrogram of a section of a typical North Atlantic blue whale song indicating all four unit types that occur in the North Atlantic: monotonic (A), downsweep (B), hybrid (C) and 9-Hz (D) unit.

Recordings were made at a sampling rate of 1kHz using an array of five autonomous bottom-moored recording units referred to as "pop-ups" (Cornell University, Bioacoustics Research Program (CUBRP), Ithaca, NY, USA) (Clark et al., 2002; Clark & Clapham, 2004), placed 2 km apart at depths of 60 – 100m in a "W"-formation (Fig. 2). Prior to deployment, we synchronised the units at GPS time (GMT-05:00) to allow correction of clock drift in the system as well as precise synchronisation of multiple units in an array. Throughout the recording season, during periods with no animal sightings, we collected GPS positions of known sound sources (e.g., light bulb breaks), which were used to validate the location accuracy of the array. When possible, we calculated locations of singing whales from the arrival-time-differences of their calls as recorded across the array using an extension of XBAT (version 6.1.0.1, Figueroa & Robbins, 2008; www.xbat.org), a specialised acoustic analysis program written in MATLAB (version 7.0.4, release 13, The Mathworks, Natick, Massachusetts, USA) and developed by the CUBRP.

Acoustic Data Processing

Acoustic data were visualised as continuous 24h-spectrograms using XBAT. Recordings were first scanned for monotonic and downsweeping song units using the template detector, an extension in XBAT (Brandes *et al.* 2006) and subsequently browsed manually to delete false positive detections and log each song unit of all types individually. When the same song was visible on several channels, units were only logged in one, in order to avoid multiple counts. We used standardised display settings to reduce variation in the accuracy of the frequency and time resolution. Spectrograms were calculated by Fast Fourier Transform (FFT size: 1024 points; Hanning window; window size: 2.1s with 80% overlap). This song unit detection and logging procedure was not carried out for all recording days but we chose two sub sampling methods for the two different questions. On the one hand, for the analysis of seasonal song unit output, we processed the recordings every 72h (same procedure for both recording years) over the entire recording period, starting the first day of recordings in 2004 and the 4th day in 2005 (time period for both years: July 18th to October 17th). On the other hand, for the analysis of types of song unit outputs in relation to the social context, we only selected those days for which we had simultaneous field observations on, or close to the array. This ensured that potential vocalisations of the animals observed at the surface were recoded on multiple units.

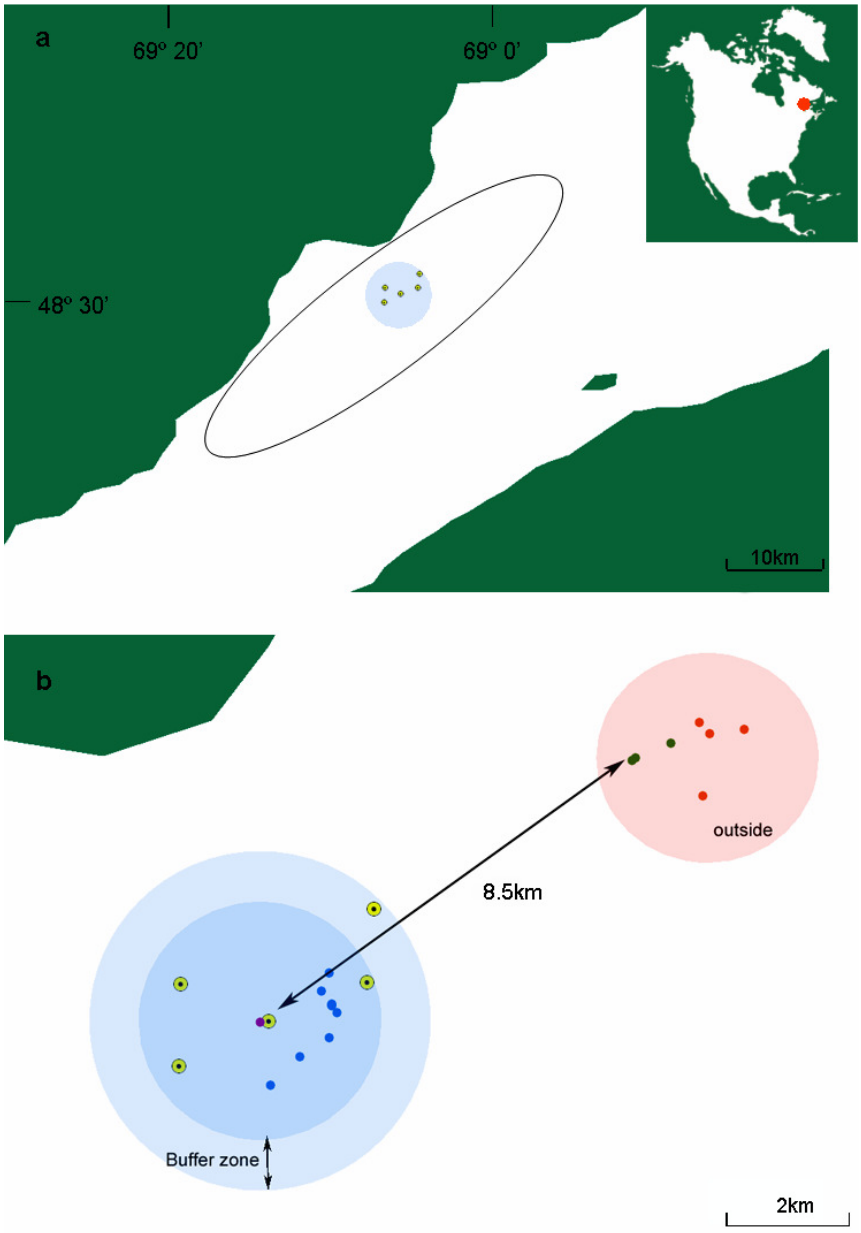

Fig. 2. (**a**) St Lawrence Estuary study area and map of North America showing the location of the St Lawrence Estuary (red dot). Ellipsis shows typical survey area, yellow dots indicate locations of the pop-ups with observation area example (light blue circle). (**b**) Magnification of section around the pop-ups. Internal light blue circle represents an example of a 2km observation range surrounded by a pale blue circle indicating the buffer zone. Blue dots represent a track of a travelling blue whale. The magenta dot at the centre represents the GPS position of a stationary whale. Red circle surrounds GPS positions of two blue whales (red & green dots) outside the 2km observation range. Example from the 4 September 2004 dataset.

Visual Observations

Under suitable weather conditions, we conducted visual daily observations during boat-based surveys (one to two 7m rigid-hulled inflatable boat). At each whale encounter we noted the number of whales, potential associations (i.e., between females and males, mother and calf), GPS time and position (distance and bearing) relative to the boat of each animal in sight at each surfacing after a dive. Animals that were further away and only identifiable by their respiration spouts, were also noted. When blue whales were encountered on the pop-up recording area, we additionally employed a focal sampling procedure for individual whales to get visual tracks of their movements. These tracks were composed of GPS coordinates corresponding to the individual's diving positions (recognisable as distinctive swirls at the water surface). Furthermore, we took photos of the animal's body coloration pattern and markings for photographic identification (including sex if known). When possible, we attempted to conduct these focal observations for all animals (usually between 1 and 6) within the visible range (approx. 2km) of the boat in the recording area. The duration of focal follows comprised either three to five surfacing periods, defined as blow cycles, or 30min to 1h in case the animals were feeding at the surface. Besides the dives and blow cycles, we also noted the orientation of each animal when surfacing as well as general behaviours including travelling (i.e., swimming with constant speed and direction), moving (i.e., short-time rather erratic movements with no constant speed), surface feeding (i.e., typical lunge-feeding behaviour observed at the surface when prey items are in the upper water column), stationary feeding (i.e., regular diving behaviour accompanied by a stationary circling swimming pattern during the blow cycle, probably on top of a food patch), social behaviour (i.e., aggressive encounters, female-male interactions), and "unknown" (when not identifiable).

Song Unit Production and Inter-sexual Associations

To describe the onset of song unit production and seasonal variation, we performed hourly counts of song units (every unit of each of the four types) for each processed day, and setting sunrise as the starting point. We combined the two years and averaged song unit counts over single months (Table 1). Furthermore, to each processed day we also assigned the total number of animals sighted, the number of single whales as well as female-male associations (called 'pairs' to simplify) and calculated monthly averages (Table 1).

Table 1. Summary (mean ± standard error) of monthly song unit production, presence of pairs and total number of blue whales (tot Bm). N represents the number of days per month (2004 and 2005 combined)

	N	Song units ± SE	Pairs ± SE	tot Bm ± SE	Pairs/tot Bm ± SE
July	14	0.00	0.00	2.75 ± 0.48	0.00
August	31	103.30 ± 29.76	0.29 ± 0.17	4.06 ± 0.33	0.07 ± 0.04
September	30	408.52 ± 51.67	1.13 ± 0.18	4.84 ± 0.42	0.23 ± 0.03
October	17	567.67 ± 184.10	2.43 ± 0.55	7.86 ± 1.62	0.31 ± 0.05

To investigate diel variations in the production of songs and fragments, we plotted the sum of hourly counts of each unit output type for the days selected for the social-context analysis (see Acoustic Data Processing; Table 2 as Appendix). We defined songs as stereotypic repeated phrases of units lasting at least 10 minutes, and fragments as single song units or non-patterned short sequences of two to five units. Since songs can last several hours, the time of song start was considered for the hourly count.

Matching of Acoustic Recordings and Visual Observations

We only used datasets where visual observations coincided with acoustic recordings, in time and space (i.e., field observations on pop-up area). Acoustic locations were x-y coordinates in metres relative to a reference point (GPS coordinates of a pop-up). Locations of single units or fragments, and tracks of songs were converted into GPS coordinates to be matched with surface GPS positions and visual tracks of focal whales. Only song tracks could be unequivocally attributed to a focal whale (if we were following it while it was singing), whereas single units or fragments could rarely be assigned to a specific individual. The reason for this difference is that songs are produced over a long time span that also includes several surfacings (seen as silent gaps in the recordings). Consequently, the coincidence of the acoustic gaps with the observations at the surface combined with the matching of multiple surface positions with the acoustic tracks allowed to identify singers. However, when multiple animals were within a couple of hundred meters and one of them emitted a single unit or a fragment, the localisation-precision of the array was not sufficient to clearly identify the signaller.

To each GPS point taken for the field protocol, we associated the time and the visual observations made: ID and sex (if available) of focal whale; distance, bearing, association (e.g., single or in pair), ID and sex (if available) of other animals (single or pairs), behaviour

of focal animal, general behaviour of focal 'group' (if identified), and comments. We plotted all positions in ArcMap (ESRI, ArcGIS Version 9.2) and defined a range of 2km, which approximately equalled the visual range from our boat for every hour of observation (clock hour start). All analysis were then based on these hourly observations made within a visual range of 2km. However, when the focal group for example dispersed and thus passed the 2km range of a few hundred up to about 1km (buffer zone, Fig.2), it was still considered as being within the 2km range metric. Everything outside this buffer zone was considered as being outside (usually >> 4km from focal animals) (Fig. 2).

Statistical Analysis

The database for the analysis presented here was the same, but statistical tests were performed separately for songs and fragments. The database consisted of an entry for each hourly observation (as described above) that was defined as a block (block 1 = 8:00-9:00, block 11: 18:00-19:00 Eastern Time). In total we had 52 1h-blocks. Entries associated with each block included: Year, Julian calendar day (Day), number of fragments, presence/absence of fragments, number of songs, presence/absence of songs, total number of blue whales (Bm.tot), number of single whales (Single), number of pairs (Pairs), number of males (Males), number of females (Females), number of songs outside 2km (Songs.out), number of fragments outside 2km (Fragments.out), general behaviour (if available) (Table 2). We grouped the 12 days used for this analysis into three blocks of four days each (Periods) representing the time span from the seasonal onset of song unit production until the end of the recording period (i.e., Beginning, Centre, End) (Table 2). Because we did not always know the sex of all the animals we were observing, we created a variable with three levels for the number of females and with two levels for the number of males. If no females were present, we assigned a "0" (level 1), when exactly one or minimum one female was present, we assigned a "1" (level 2), and when exactly two or minimum two females were present, we assigned a "2" (level 3). 'Females' comprised both single females as well as females in a pair. Since in all blocks there was at least one male, we assigned a "1" when exactly one or minimum one male was present, and a "2" when exactly two or minimum two males were present. We defined a song as being outside 2km, when the singer was located outside of our 2km observation range, or when it was audible but not locatable because too far away. The number of fragments and songs outside the 2km range gave an estimate of the presence of vocally active males in the area that were detectable by the focal animals and could thus have influenced the vocal behaviour of the latter. Since females do not emit infrasonic units and only rarely and sporadically other types of vocalisations (i.e., calls) produced by both sexes

(Di Iorio, unpublished data), their presence could not be estimated acoustically. This little vocal activity combined with the limited visual range suggest that the focal animals were only marginally aware of their presence and that these distant females could only have a limited direct effect on the acoustic behaviour of the focal males. Females outside the 2km observation range were thus not included in the analysis. However, to have an idea of the presence of the animals outside the 2km focal observation range, we used sightings made during the daily surveys in the areas surrounding the focal pop-up area (see Visual observation section, Fig. 2). Since we could not scan the surrounding area continuously, even when both boats were on the water, we were not able to determine the number of blue whales outside the 2km for each 1h-block. Nevertheless, this procedure enabled us to estimate the distribution and density of the animals during the observation days. Finally, we did not include behaviour in the statistical analysis because it was often too general and not clearly identifiable for each block. For example, singers could be followed, whereas fragment-producing whales could not and if they occurred at the same time, defining one general behaviour would not have considered both signaller types. Furthermore, it was either a description of the general behaviour seen at the surface by the observed 'group' that did not include potential individual behavioural differences or changes in behaviour, or the behaviour of the focal animal. Nevertheless, we described the behaviour of vocalising individuals for whom we had visual tracks and we descriptively compared the general behavioural contexts of the animals present with and without song respectively fragment production as well as between cases of song versus fragment production.

Does the audience influence the production of songs and fragments?

To understand how the audience influenced the production of songs and fragments, first of all, we determined how the following variables affected the probability that songs or fragments were produced within a block: Bm.tot, Single, Pairs, Females, Males, number of fragments/or songs, Fragments.out, Songs.out. Bm.tot consisted in the sum of Singles and Pairs present and was therefore omitted from the analyses.

Because songs showed a more quasi-binomial distribution whereas fragments a quasi-poisson distribution, we used two different statistical models with error structures reflecting this difference. Furthermore, in order to control for repeated measurements, we had to fit Year, Period and Blocks as random terms. The best applicable model for this kind of design is a multivariate generalised linear mixed effects model (GLMM) (Venables & Ripley, 2002). However, since our sample size, 52 blocks, was not sufficient to carry out an analysis with

Blocks nested in Period, nested in Year, we first tested whether each of these factors had an effect on the production of either songs or fragments by conducting a quasi-logistic regression for 'songs' (glm function) and a quasi-poisson regression for 'fragments'. Only significant factors were later included in the final models.

Since correlation among predictor variables has to be avoided, we explored the existence of multicollinearity among our predictor variables by calculating a variance inflation factor (VIF) for each variable. A VIF of five or greater indicates the presence of multicollinearity (Heiberger & Holland, 2003). Since non of the factors (Year, Period, Block) had an effect on song production, the final model was a multivariate generalised linear model (GLM, glm function with logit link for quasi-binomial data) with the social variables as covariates and no random terms. To test the effect of the variables on fragment production, we conducted a multivariate GLMM (glmmPQL function, with logit link for quasi-poisson data) with the social variables as covariates and with Period (only factor with significant effect) fitted as random term to control for seasonal effects.

RESULTS

Seasonal Variation

For both years combined, we used a total of 14 days in July, 31 days in August, 30 days in September and 17 days in October adopting the 72h-method. The seasonal variation of song unit output combined with sightings of female-male associations revealed a clear increase in song unit production over time, with no song units recorded in July (Fig. 3). The onset of song unit production occurred in the second half of August (around 20 August). Similarly, there was an increase in female-male associations over time, with most pairs observed in October, and none sighted until the second half of August (Fig. 3).

Diel Variation of Songs and Fragments

Fragment and song production followed different diel trends. The number of songs produced over the day did not show important fluctuations, contrarily to the number of fragments that showed a clear increase during the daytime hours and a decrease before sunrise and after sunset (Fig. 4).

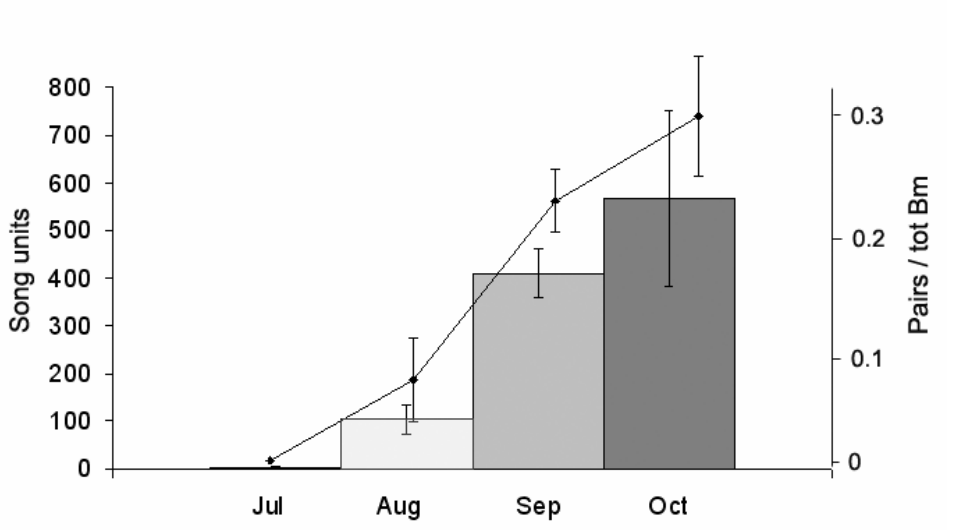

Fig. 3. The bars represent the seasonal variation of song unit output as monthly means ± SE of song unit counts corrected for the mean number of blue whale sighted each month. The superposed line represents the mean ± SE of female-male association (Pairs) sightings per month corrected for the monthly mean of the total number of whales (tot Bm) sighted. The time span was 18. July to 7. October (2004 and 2005 combined). The number of days used per month is summarised in table 1.

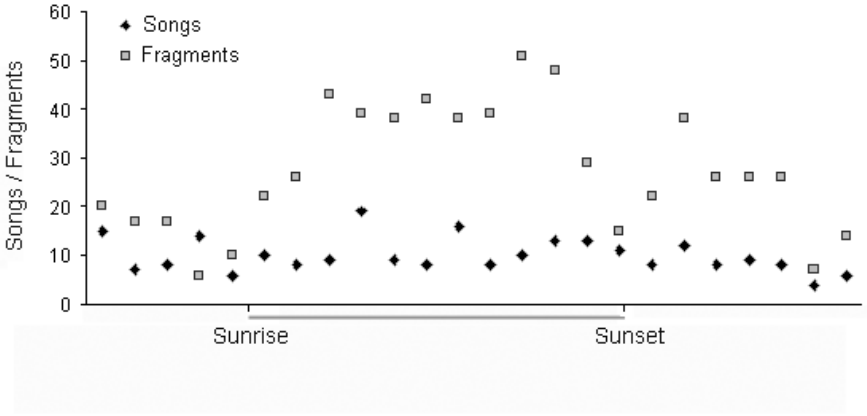

Fig. 4. Diel variation of the hourly counts of songs (black rhombi) respectively fragments (grey squares) produced. The grey bar indicates daylight hours. The days used are listed in table 2.

Social Context and the Production of Song and Fragments

All variables showed a VIF smaller than five and were therefore used in the final models. Neither Year nor Periods nor Blocks had a significant effect on the probability of emitting songs (GLM $_{Year}$, d.f. = 1, Wald χ^2 = 0.128, P = 0.72 ; GLM $_{Periods}$, d.f. = 2, Wald χ^2 = 3.17, P = 0.23; GLM $_{Blocks}$, d.f. = 51, Wald χ^2 = 0.94, P = 0.35) and were thus not included in the final model. The number of songs produced within blocks was not significantly associated with any variable, but tended to be related to the number of single whales within 2km (Table 3). Because fragment production showed no effect of Year nor Blocks (GLM $_{Year}$, d.f. = 1, Wald χ^2 = 1.47, P = 0.27, GLM $_{Blocks}$, d.f. = 51, Wald χ^2 = 0.20, P = 0.80) but of Periods (GLM $_{Periods}$, d.f. = 2, Wald χ^2 = 8.13, P = 0.02), the final GLMM was performed with Periods as random term. Fragment emission was significantly, positively affected by the number of females and single whales present in the 2km range (Table 3).

Table 3. Results of final GLMM for songs and fragments showing P values and Wald χ2 test for each independent variable used in the two models.

Variables		Single	Pairs	Females .level2	Females .level3	Males. level2	Fragments.2km / Songs.2km	Songs.out .2km	Fragments. out.2km
Songs	P	*0.056*	0.39	0.43	0.25	0.70	0.72	0.99	0.94
	χ2	1.91	1.87	-0.80	-1.17	0.39	-0.36	-0.009	0.08
Fragments	P	**0.03**	0.50	**0.047**	**0.028**	*0.052*	0.49	0.097	0.35
	χ2	-2.29	-0.67	1.987	2.27	1.99	0.69	-1.69	-0.94

Significant terms highlighted in bold, tendencies in italic. N = 52. Abbreviations: Females.level2 = 1 ore more than 1 female, Females.level3 and Males.level2 = 2 or min. 2 females or males. Model numerator df = 1, denominator df = 42.

Behavioural Context

Overall, blue whales within the focal 'group' were mainly feeding (40-60% of general behaviour). The rest of the time they were either socially interacting (7 – 20%) or moving (11-16%) (Table 2). From the acoustic tracks, for six of which we had concurrent surface GPS positions and observations, song producing animals were travelling, sometimes roaming through the area for a while (approx. 10 to 30min) and then leaving. A direct comparison between the general behaviour of the focal 'group' between song and no-song production could not be made because there were only 11 blocks with songs against 41 blocks without

songs (Table 2). However, the striking difference was that when songs were produced, no obvious social behaviour neither moving was observed in the focal blue whale 'group', and during 60% of the time animals were feeding (Table 2). In the case of fragment emission, the main difference observed was that the animals were almost three times more often engaged in social interactions in the presence than in the absence of fragments (Table 2). In 20% of the cases, it was not possible to identify the general behaviour although the animals were relatively stationary within the area and mainly feeding. Furthermore, during fragment production events, blue whales were more engaged in social interactions and moving compared to song production events.

DISCUSSION

The aim of this study was to investigate the functional significance of patterns in song unit output. Because changes in vocal behaviour in relation to the audience have often been used as indicators of signal function (Catchpole, 1973; Andersson & Iwasa, 1996; Bradbury & Vehrencamp, 1998), we put particular emphasis on the social environment of vocal production although, in conjunction with the behavioural context. We found that the two song unit outputs were differently affected by the potential audience. Song production was not influenced by any of the variables describing the social environment, whereas fragment emission was mostly affected by the close presence of females and single whales. We also found that the seasonal onset and variation in song unit production followed a parallel trend with the onset and variation of female-male associations. Both started in the second half of August and increased during the course of the summer/autumn season.

The coincidence of the onset and parallel increase of song unit production and pair sightings does not necessarily represent a causal relationship. However, the change in the social context (pair formation) co-occurs with the change in song unit production and both behaviours are potentially linked to mate choice and reproduction. The occurrence of these two behaviours at the end of the feeding season might prelude the reproductive season. Other behaviours typically involved in mate choice, for example agonistic encounters, have also been reported during the same period (Sears et al., 1990; Berchok et al., 2006). Female-male associations and singing during the feeding season have been described for other balaenopterid whales such as humpback (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*) (Clapham, 1996; Croll, 2002; Clark & Clapham, 2004). The authors

suggest that singing in high latitudes represents a low-cost advertisement by males that can be used by conspecifics to assess a potential mate or opponent. They also suggest that it represents a reproductive strategy by males to establish bonds with females early and propose, in particular for fin and potentially blue whales, that these displays serve to attract females from great distances to aggregations of patchily distributed prey. Song and fragment emission was not present up to the end of the summer, despite the presence of males in the area. This may indicate that feeding is the primary activity up to that time and that behaviours linked to advertisement and mating such as singing, only start when a certain amount of energy has already been stored or as a preamble to breeding (e.g., changes in sexual hormones' levels) (Clutton-Brock & Albon, 1979; Evans & Marler, 1994; Hau et al., 2000; Rashotte et al., 2001; Malo et al., 2009). This also suggests that singing could be costly, which would further support the hypothesis that songs represent sexually selected traits (Clutton-Brock & Albon, 1979; Zahavi, 1982; Andersson & Iwasa, 1996). A conflict between singing and feeding is particularly known in birds (e.g., Dall & Witter, 1998) but has also been shown in blue whales by the fact that song production occurred at shallow depths while travelling and never while feeding at depth (Oleson et al., 2007). Early vocal display may therefore be linked to better male condition and play a role in mate choice, as demonstrated in species with seasonally reproductive cycles such as in birds or deer (Cuthill & Macdonald, 1990; Arvidsson & Neergaard, 1991; Otter et al., 1997; McElligott et al., 1999; Poesel et al., 2006). Peaks of singing by blue whales have been reported during twilight and night hours concomitant with the vertical migration and dispersion of their prey that might result in less efficient feeding (Stafford et al., 2005). We did not find a similar diel singing pattern but this might be due to the fact that the period we observed was much shorter, the recording area more constrained and the number of days analysed considerably smaller than in the other study. However, we found an opposite diel trend for the production of fragments of song units, with a clear increase and consistent amount of fragment production during the day, between dusk and dawn (Fig. 4). This is also the period of time during which prey usually occurs in dense patches at greater depths (100-200m), where singing usually does not occur (Stafford et al., 2005; Oleson et al., 2007). The production of fragments instead of songs might therefore be energetically less demanding, as suggested by Oleson and colleagues (2007).

The conflicting relationship between patterns of song output and food consumption emphasises the role of the social environment, particularly if song unit emission is involved in reproductive behaviour. This is further supported by the findings that in 73% of the cases with observed social interactions, fragments were produced and that fragment emission was

positively affected by the number of single animals in the focal area. Furthermore, we found a strong effect of the number of females on the production of fragments, in particular when minimum two females were present. Most of the time we could not locate who was emitting the fragments and thus ignore if one male was more vocally active or if several males were producing fragments. From some locations and time of arrival differences, it seemed that if an individual produced fragments, it did so repeatedly. Whether the primary receivers were other males, the females present or a particular individual cannot be unequivocally determined. However, the presence of both close males and distant singing males had no effect on fragment production, which suggests that the primary receivers were the females. As shown across species, if male vocal production was related to intra-sexual interactions, for example to defend resources, the vocal activity would have increased in the presence of other males (Galeotti et al., 1997; McElligott et al., 1999; Wich & Nunn, 2002; Davidson & Wilkinson, 2004; DuBois et al., 2009).

It has been proposed that fragment emission is used by males in a pair to maintain the bond with the female while feeding at depth (Oleson et al., 2007). We do not exclude that this may be a function of fragments since in 80% of the cases with fragment occurrence we observed, pairs were present. In the other 20%, fragments were produced in the presence of multiple females. This suggests that fragment production is not only related to already established female-male bonds but might also be directed towards single females, possibly to initiate interactions that may lead to bonding, or to advertise a male's presence and status. Indicative for this supposition is the fact that individual males can be distinguished and potentially recognised by their emitted fragments only, as shown by the clear individual differences found in the acoustic structure of the predominant fragment unit type (the monotonic unit) (chapter 1). In many animal species with vocal reproductive displays, female preference and mate choice decisions have been shown to be tightly linked to vocal cues (Gerhardt, 1992; Searcy & Yasukawa, 1996; Davidson & Wilkinson, 2004; Puts, 2005; Castellano & Rosso, 2007; Charlton et al., 2007; Clutton-Brock & McAuliffe, 2009).

Fragments were mainly emitted in a stationary behavioural context (e.g., stationary or surface feeding) in which visual inspection and physical contact between senders and receivers were likely possible. Consistent with this notion are our frequent observations of approaches between individuals and social interactions that appeared to be related to pair formation. In such a situation, the exigency to produce long and potentially costly unit sequences might be reduced. Alternatively, another reason for producing only fragments

instead of patterned sequences of song units might be that the proximity of conspecifics restrains the production of unit sequences. For example, singing humpback whales that were approached by another male have been observed to cease singing, although they continued to sing when escorting a female (Smith et al., 2008). In many bird species, the close presence of females causes a reduction in singing behaviour and solitary or unpaired males stop singing once they form a bond with a female (e.g., Catchpole, 1973; Breitwisch & Whitesides, 1987; Dunn & Zann, 1997). Similarly, unmated male gibbons (*Hylobates Lar*) have been described to call more often and extensively than mated males (Raemaekers et al., 1984), and male orangutans (*Pongo spp*.) call more when alone than when guarding a female (Mitra Setia & van Schaik, 2007). In blue whales, one male was reported to start singing after dissociating from a female (Oleson et al., 2007). This might explain why song production was not affected by any of the variables describing the audience. Singers were not stationary and travelled through the area, thus suggesting that singing is an undirected behaviour. This is further supported by the fact that singing blue whales have been reported to be "solitary", not in direct proximity and out of visual sight of other conspecifics (Oleson et al., 2007). Undirected singing could be used to attract females from a distance (Searcy & Andersson, 1986). Individual differences in multiple traits of the blue whale song structure have been described and potential mates might use them to identify and assess males from a distance (chapter 1). Furthermore, since songs are long-range displays with a high degree of repetition of unit sequences, the locatability of the singer is enhanced, thus facilitating a potential mate to join the singer (Bradbury & Vehrencamp, 1998). This kind of repetition of sequences might not be necessary at close ranges, where visual and physical contact are possible. Finally, the fact that the singers we followed were active during the day, when others feed at depth, could also be an indication of quality since only high-quality males might afford to sing on the expenses of feeding (Zahavi, 1975; Lailvaux & Irschick, 2006) . However, our data do not allow us to elucidate these kind of relationships, although this would be a fruitful field for further research.

In conclusion, our study suggests that the emission of song units in blue whales is linked to reproductive behaviour and that despite the limiting factor of food consumption in the production of long unit sequences, the different types of song unit outputs are involved in different social contexts. As we suggested, song production appears to be undirected and suitable for advertising while travelling in a variable dispersed social environment, where the position and identity of potential listeners are not know. In contrast, in a stationary situation, where signallers and receivers are congregated within potential visual sight and inspection

distance, song units are mainly emitted singularly or in small fragments. Furthermore, this limited vocal output may enable individuals to advertise themselves and engage in social interactions without impairing food intake. This study also suggests that the primary receivers of song unit outputs are the females and it provides new insight into the use and possible function of song unit patterns. It also suggests that investigating song production in an area of conflicting interests (feeding vs. courtship behaviour) might be fundamental to understand mate choice in blue whales. Further studies are needed in summer feeding as well as wintering areas to shed light on the role of song unit output in mate choice and sexual selection in general.

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APPENDIX

Table 2. Summary of variables used for the social-context analysis of song and fragment production, represented as averages per Periods in the case of scalar variables and percentages in the case of categorical variables.

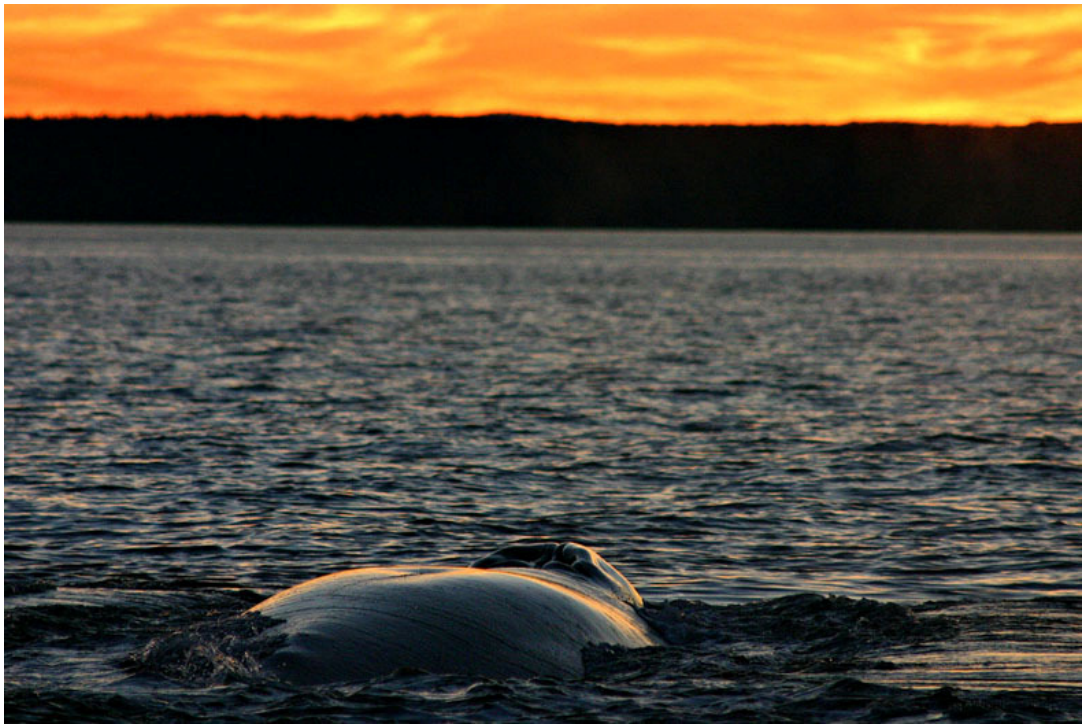
Output type		Period	nr Blocks/Year		Frag.	Frag.out	Songs	Songs.out	Bm.tot	Pairs	Single	Males		Females			Behav focal group			
			2004	2005								level1	level2	level0	level1	level2	stf	s	m	u-id
Songs	yes	Beginning	4	0	0.50	0.25	1.25	0.00	1.75	0.00	1.75	4	0	1	3	0	1	-	-	3
		Centre	1	1	0.50	0.00	1.00	0.00	3.50	1.00	1.50	1	1	0	2	0	2	-	-	0
		End	1	4	1.60	0.40	1.20	0.00	4.40	1.40	2.00	2	3	0	1	4	4	-	-	1
		Avg song			**0.87**	**0.22**	**1.15**	**0.00**	**3.22**	**0.80**	**1.75**	**63.6%**	**36.4%**	**9.1%**	**54.5%**	**36.4%**	**63.6%**	-	-	**34.4%**
	no	Beginning	13	0	3.29	0.50	-	0.21	1.93	0.50	1.07	9	4	5	6	2	6	3	2	2
		Centre	8	7	1.19	0.19	-	0.00	3.06	1.00	1.06	9	6	0	8	7	6	4	3	2
		End	2	11	0.23	0.38	-	0.00	4.54	1.46	1.62	9	4	0	5	8	6	-	1	6
		Avg no-songs			**1.57**	**0.36**	**0.00**	**0.07**	**3.18**	**0.99**	**1.25**	**65.8%**	**34.2%**	**12.2%**	**46.3%**	**41.5%**	**43.9%**	**17.1%**	**14.6%**	**24.4%**
Frag.	yes	Beginning	8	0	3.22	0.89	0.00	0.25	2.33	0.67	1.13	5	3	2	5	1	2	3	1	2
		Centre	4	5	2.22	0.11	0.11	0.00	3.22	1.00	1.22	3	6	0	3	6	4	2	2	1
		End	1	7	1.38	0.25	0.75	0.00	4.63	1.50	1.88	3	5	0	2	6	5	-	1	2
		Avg frag.s			**2.27**	**0.42**	**0.29**	**0.08**	**3.39**	**1.06**	**1.41**	**44.0%**	**56.0%**	**8.0%**	**40.0%**	**52.0%**	**44.0%**	**20.0%**	**16.0%**	**20.0%**
	no	Beginning	8	0	-	0.57	0.29	0.57	1.43	0.00	1.71	6	1	4	2	1	5	-	1	2
		Centre	6	3	-	0.22	0.11	0.00	3.00	1.00	1.00	7	2	0	7	3	4	2	2	1
		End	2	8	-	0.50	0.00	0.00	4.18	1.36	1.60	8	2	0	4	6	5	-	-	5
		Avg no-frag.s			**0.00**	**0.43**	**0.13**	**0.19**	**2.87**	**0.79**	**4.31**	**77.8%**	**22.2%**	**14.9%**	**48.1%**	**37.0%**	**51.8%**	**7.5%**	**11.1%**	**29.6%**

In bold averages or percentages over the entire period used for the analysis. Yes / no indicate events with or without song respectively fragments (frag.). Beginning (August 20, 21, 24, 28), Centre (September 5, 9, 13), End (September 17, 21, 28). Blocks/Year are the number of hourly blocks per year used to calculate the mean values of the variables per Period. Abbreviations: level 0= no females, level 1= 1 or min 1 male/female, level 2 = 2 or min 2 males/females; stf: stationary feeding, m: moving, u-id: unidentified behaviour. Behav focal group is referred to the general behaviour of the group of animals observed during the 1h blocks. Individual behaviours such as travelling by all singing whales, are not included.

CHAPTER 4

Exposure to seismic activity alters blue whale acoustic communication

Biology Letters (under revision)



Exposure to seismic activity alters blue whale acoustic communication

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ABSTRACT

The increased demand for energy has resulted in the growth of exploration for oil and gas in the marine environment over the last decade. The high intensity and peak frequency band of seismic survey sounds are likely to interfere with the acoustic signalling of large whales. However, our knowledge about the interference of seismic sounds with baleen whale acoustic communication is sparse. We investigated whether blue whales (*Balaenoptera musculus*) changed their vocal behaviour during a seismic survey that deployed a low-medium power technology, referred to as a sparker. We found that whales called consistently more during periods with the sparker operating than without. This increase was observed for the audible, frequency-modulated calls that are mainly emitted during social encounters and feeding. This response presumably represents a compensatory behaviour to the elevated ambient noise from seismic operations. Surprisingly, it occurred at relatively low levels of seismic noise exposure, suggesting that whale behaviour is potentially affected over a large spatial area.

INTRODUCTION

Marine exploration surveys rely primarily on systems that produce impulsive (< 50ms) and high intensity (190 to over 250dB re 1µPa-m, peak-to-peak) sounds, with most energy below 200Hz (McCauley et al. 2000). The frequency band of major energy for these sounds overlaps the acoustic signals and estimated hearing ranges of baleen whales (Ketten 1992). Whales and dolphins rely on sound production and perception for vital activities such as navigation, food detection, and social communication (e.g., maintenance of social cohesion, reproductive behaviour) (Tyack & Clark 2000) and interference with their signalling system could thus have serious implications for individuals and populations.

Blue whales emit two major types of vocalizations: redundant, patterned sequences of infrasonic sounds (songs, 8-100Hz) that are probably used for long-range communication (Payne & Webb 1971; Tyack & Clark 2000) and frequency-modulated audible sounds (calls, 30-200Hz) that are mainly emitted during close social encounters and feeding (Berchok et al. 2006; Oleson et al. 2007). These calls are discrete, transient and two to three times less intense than infrasonic song units (Berchok et al. 2006). Because of their acoustic characteristics, including short duration [1-4s], frequency band, transient and discrete nature, calls might be particularly susceptible to interference from long trains of seismic survey sounds (Fig. 1).

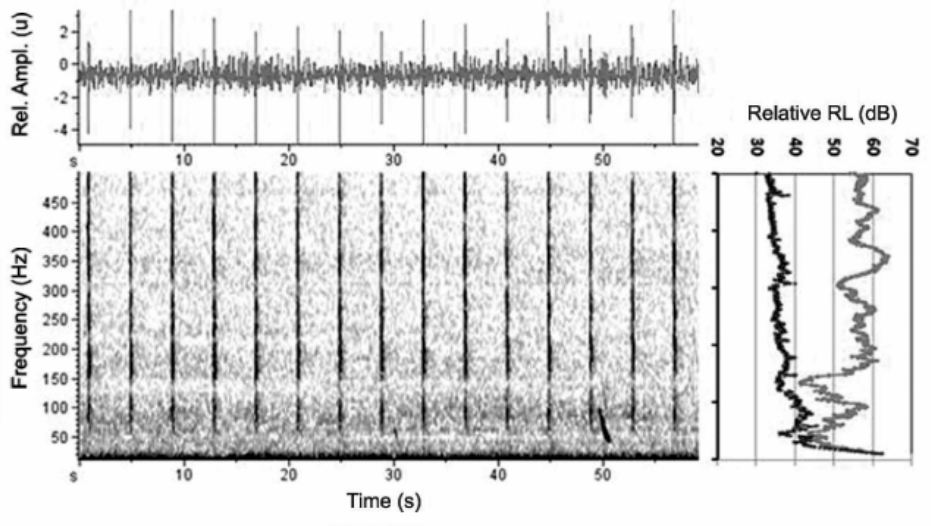

Fig. 1. Waveform (top), spectrogram (bottom), and average spectrum distribution in the 0–500Hz band (insertion) of a typical mid-frequency blue whale call and seismic sparker pulses (black lines) (pulse duration: 16.2ms, inter-pulse-interval: 4s, peak frequency: 163Hz). (Hanning, 1024pt. FFT, no overlap, sampling frequency = 1000Hz).

To investigate whether blue whales adjusted call production when exposed to seismic operations relative to natural conditions, we compared calling activity during days with seismic operations and without. Furthermore, since during the seismic survey days, seismic activity was intermittent, we used noise-free periods, when the seismic ship was not operating, as controls and compared calling activity within these periods with the seismic exploration periods.

METHODS

Data Collection and Processing

Data were collected in the St. Lawrence Estuary (SLE) (Qc., Canada), where blue whales congregate during the summer to feed. From 1-11 August 2004, some of these whales, which are part of a long-term visual-acoustic project, were subject to seismic sparker operations (low-medium power technology) (Bellefleur *et al*. 2006). During the entire survey period, we sighted 39 blue whales, with the same individuals often re-sighted over several days.

Acoustic recordings were made using an array of five, bottom-mounted autonomous acoustic recorders, separated by 2km, and operating continuously at 1kHz sampling rate (Clark & Clapham 2004). We complemented these acoustic data with daily boat-based visual surveys, to document which whales were present, and to determine relative abundance and general behaviour. The seismic operations were conducted only on four days in our research area, and seismic sounds were clearly detectable on all five recorders.

We examined the spectrograms of each sound file of all eleven survey days and noted blue whale audible calls as well as periods with seismic activity. All calls were detected within the recording area (ca. 3km range per recording unit) and most calls (77%) were acoustically located within the array. The estimated received levels for seismic events at the recorders (60-100m depth) were calculated using the RMS levels of the events and the calibration specifications of the recorders.

Analysis

We divided the four days with and four days without detectable seismic activity into 10-minute windows, considering time of day and correcting for daylight proportions: daytime

(corresponding to 54% of all windows), night time (33.5% of all windows) and twilight (calculated as sunrise or sunset ± 1.5h; 12.5 % of all windows). Because call production also depends on the number of animals present in the area, the model should be corrected for it. However, since we did not know the precise number of whales present throughout the day, we assigned presence (1) or absence (0) of call detections to each window. For the comparison between days with seismic survey activity (seismic) and days without (no-seismic), we performed a 10-fold cross-validated binary logistic regression with 888 randomly chosen 10-minute windows out of 1296 (444 seismic days, 444 no-seismic days). Within the four survey days, there were also periods with no seismic sounds present. We used the same type of model and validation to compare 172 seismic periods and 172 no-seismic periods out of 447 within the days with detectable seismic activity.

To evaluate whether the onset of seismic testing influenced whale vocal behaviour within the four days with seismic noise, we chose blocks of at least 1h with seismic sounds that were preceded by 1h blocks without seismic sounds. We counted the number of calls within these 1h blocks and compared 1h time block pairs (7 pairs in total) with and without seismic activity using a paired Wilcoxon signed rank test.

RESULTS

Between-days Analysis

Blue whales emitted significantly more calls on seismic than on no-seismic days (N=888, $\chi 2 = 12.975$, $P < 0.0001$) (Fig. 2a). Vocal activity was also dependent on time of day (N=888, $\chi 2 = 38.701$, $P < 0.0001$). The dial pattern of vocal activity was similar for both conditions, but whales called significantly more often when exposed to seismic sounds, independent of time of day (Fig. 2a).

Within-days Analysis

Within the seismic survey days, blue whales generally called more during periods with seismic explorations than during noise-free control periods (N=344, $\chi 2 = 3.55$, $P = 0.059$). This response appeared to be dependent on the time of the day (N=344, $\chi 2 = 6.8$, $P = 0.03$), with significant response differences during twilight and daytime hours (Fig. 2b). Relative to the control periods, blue whales called most in the presence of seismic noise during twilight, which also had the highest proportion of overall seismic activity (56%). A significant increase

in call production in the presence of seismic noise was also observed for daytime (32%), whereas there was a slight decrease in call production during night time, which had a very low proportion of seismic activity (12%). (Fig. 2b).

The onset of seismic activity also had an effect on blue whale call production, as revealed by the significant increase in call detections from the control no-seismic 1h blocks to the adjacent seismic 1h blocks (Wilcoxon signed rank test: N=7, Z = -2.207, P = 0.031) (Fig. 2c).

DISCUSSION

Possible short-term adjustments reported for other vertebrate taxa when exposed to increased levels of ambient noise include shifting call frequencies, increasing call amplitude, increasing call duration, increasing rate of calling, or ceasing to call until the noise decreases (Brumm et al. 2004; Slabbekoorn & Peet 2003; Sun & Narins 2005). In baleen whales, Northern right whales (*Eubalaena glacialis*) exposed to high noise from commercial shipping increase call frequency (Parks et al. 2007), while some humpback whales (*Megaptera novaeangliae*) respond to low-frequency active sonar playbacks by increasing song length (Fristrup et al. 2003; Miller et al. 2000). Our data do not allow reliable measurement of call amplitude or duration because of the high variability in received levels, the resultant inconsistency in determining the start and end times of a call as well as the high natural variability of call duration and modulation.

Audible, mid-frequency blue whale calls are transient, generally not stereotyped or repeated in patterned sequences (such as songs), and they are probably used for short-range communication in social interactions (Bass & Clark 2003; Berchok et al. 2006; Oleson et al. 2007). Increasing the production of this call type may thus increase the detectability of the signal by other whales. This is consistent with the prediction from information theory, which states that an increase in call production compensates for the masking of information by noise (Shannon & Weaver 1949). Several bird species increase call repetition rates as a short-term adjustment to interfering background noise (Brumm & Slater 2006; Lengagne et al. 1999). Our findings provide the first evidence for this type of a noise-dependent adjustment in calling baleen whales. Additional variables such as daytime or social context may have affected the calling behaviour of the blue whales we studied. However, the effect of this behavioural variability on our analysis is expected to be small because we used binary counts,

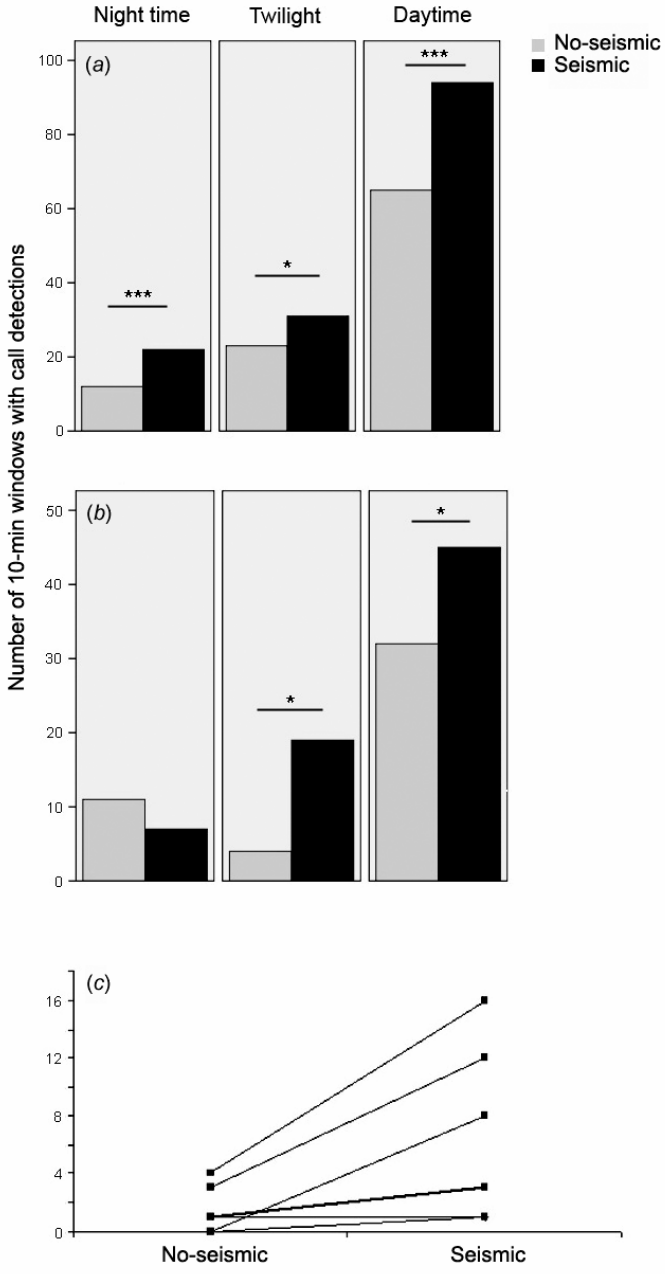

Fig. 2. Calling activity of blue whales in presence and absence of seismic noise. Comparison of 10-min windows with call detections as a function of time of day. (*a*) Days with and days without seismic operations (*** - binary logistic regression, $P < 0.001$, Brier score of 10-fold cross-validation of model = 0.19). (*b*) Seismic and no-seismic periods within the seismic survey days (* - binary logistic regression, $P < 0.05$; Brier score of 10-fold cross-validation of model = 0.2). (*c*) Number of calls during consecutive 1h no-seismic and seismic blocks. Bold line indicates that this no-seismic to seismic change occurred twice.

analysis windows were randomly chosen and daytime was included in the model. Furthermore, our choice of short, 1h pre-test and test blocks allowed us to control for daytime and animal density in the recording area.

There is one anecdotal reference to a blue whale that stopped singing when exposed to seismic noise from airguns (McDonald et al. 1995). However, the cited study describes a case of one travelling blue whale that stopped singing when it was 10km from an active seismic ship. In contrast, we found increased production of audible mid-frequency calls when seismic sparker events were present. This suggests that blue whales respond to changes in their acoustic environment depending on the context (close social contact vs. very long-range signalling while travelling) and their specific communication state (immediate and near-term vs. distant and long-term). This would further predict that for animals engaged in near-term, proximate communications there is an advantage in acoustic behaviours that maintain the immediate social link, while for animals engaged in intense singing, which is directed at a distant audience and goes on for many months, there is little to no advantage to an immediate increase in singing. Although the study could not show a compensatory response at the individual level, the clear results are in line with this explanation. However, because SLE blue whales start emitting songs only towards the end of the summer (i.e., end of August; Di Iorio, unpublished data), we could not examine how this type of vocalisation was affected by seismic survey sound. Further studies are thus needed to test this hypothesis, also with respect to different noise sources, including different seismic techniques and characteristics such as received level. In the case of the blue whale singer (McDonald et al. 1995), the source level of airgun pulses (> 215dB re 1µPa-m, peak-to-peak) was much higher than that from 8kJ sparker pulses (193dB re 1µPa-m, peak-to-peak), and the estimated sound pressure typically impinging on the whales in our research area was 116dB re 1µPa (rms) with a maximum of 145dB re 1µPa (rms).

Although these data are from an opportunistic situation rather than a controlled exposure experiment, our assessment of whale acoustic behaviour during and between seismic activities allowed testing of the hypothesis that blue whales change their vocal behaviour in response to seismic activity. A response was evident at relatively low seismic sound levels. Given that most seismic surveys utilize airgun arrays that produce signals at considerably greater source levels and can propagate much farther than sparkers, there is the potential that the observed and possibly other behavioural responses may occur over much larger areas than assumed so far, and that large portions of blue and possibly other baleen whale populations could be

affected. This suggests careful reconsideration of the levels and ranges of concern regarding baleen whale exposures to noise from seismic surveys, which is particularly relevant when the species population is seriously depleted and at high risk of extinction as is the blue whale, the largest animal ever to exist on Earth (IUCN 2008).

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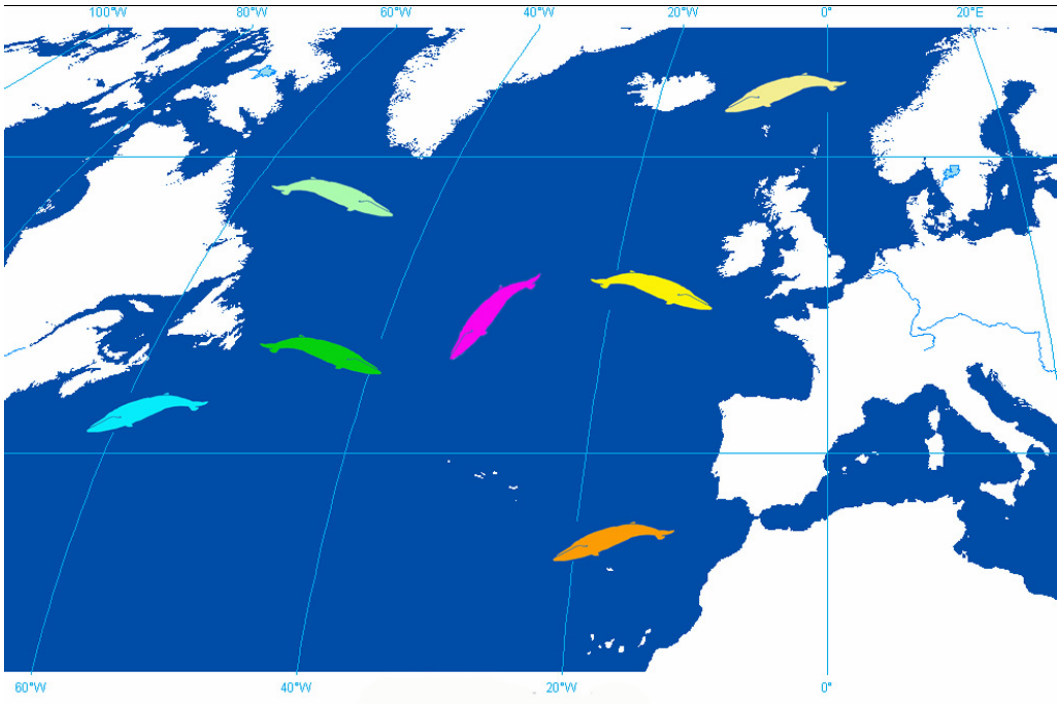
GENERAL DISCUSSION

Acoustic variability in a fluid social system



Blue whale males produce songs consisting of patterned, redundant sequences of infrasonic sounds (Cummings & Thompson, 1971; Mellinger & Clark, 2003) that are thought to represent male reproductive displays (Tyack & Clark, 2000; Oleson et al., 2007). The socio-ecological environment in which these songs are emitted is highly variable. In fact, blue whales live in a fluid social system, individuals move dispersed and in changing environmental conditions (e.g., background noise). The positions and distances between travelling individuals are highly variable, and a singer does not necessarily know who is within range as potential receiver. Furthermore, since songs can be heard at ranges of at least many hundreds of kilometres in a deep sea environment (Clark, 1995), most blue whale communication takes place within a network of a large number of senders and receivers (McGregor, 2005), almost throughout an ocean basin. This also implies that multiple singers share the same active signalling space. Altogether, this suggests that different selection pressures and factors have shaped the songs of blue whales in order to cope with such a variable environment: On the one hand at the level of the message or information conveyed in a signal ('content-based selection') that enables to assess and identify a signaller, and on the other hand at the level of transmission efficacy ('efficiency-based selection') that enables a signal to be received in the presence of environmental variability (Guilford & Dawkins, 1991).

By investigating song variability in my thesis, I aimed at better understanding the evolution and functional significance of patterns of variation in the long-range signals of a highly acoustically-oriented system, in which most communication occurs in public. Based on the results, I was also interested in formulating hypothesis about the factors shaping such variation and those altering communication. In fact, I also examined the impact of seismic noise on the production of short-ranging 'social' calls.

Individual variability

At the individual level, I found that blue whale males differed in multiple components of their songs, including song composition (proportional use of different unit types), unit rate as well as in the acoustic structure of the most common unit type (monotonic unit) (chapter 1). These findings suggest that songs convey information that can be used by conspecifics for individual identification. In the fluid, dispersed and spatial dynamic environment of blue whales, acoustic identity information might be required to set up social interactions. Although

information about the sociobiology of blue whales is rather sparse, there is evidence that individuals do not form long-term stable groups (Sears, 2008). This suggests that individual differences in the songs produced by travelling males are likely used to initiate, mediate or avoid inter-individual interactions, as observed in other (partly) nomadic species living in a fluid social environment and also producing long-distance calls such as coyotes *Canis latrans* (Mitchell et al., 2006), lions *Panthera leo* (McComb et al., 1994), elephants *Loxadonta africana* (McComb et al., 2000), chimpanzees *Pan troglodytes* (Mitani & Nishida, 1993), and bottlenose dolphins *Tursiops truncatus* (Janik et al., 2006). An important consideration that has to be made here, is that blue whale songs represent male reproductive displays that unlike most contact or group-cohesion calls have also evolved as a result of sexual selection. Singing by solitary males while travelling is therefore likely to mainly function in mate attraction or inter-individual spacing, but could also be used by conspecifics to keep track of individual male locations, for example when in search of foraging areas, or to coordinate seasonal movements. A similar explanation has also been proposed for the loud calls of the semi-solitary orangutan *Pongo spp.* males (Delgado & Van Schaik, 2000). The intense, redundant, and stereotypic songs of blue whales enable detection, location and tracking of individual males by conspecifics (Guilford & Dawkins, 1991; Bradbury & Vehrencamp, 1998). Moreover, the importance of individual vocal identity and recognition is further enhanced in a communication network where several signallers are active at the same time (McGregor, 2005). Songs are thus likely to convey information about a male's attributes such as age, status, quality, or condition as reported for mating signals across taxa (insects and amphibians: Ryan, 1991; Gerhardt, 1992; Welch et al., 1998; birds: Birkhead et al., 1998; Mennill et al., 2002; Crockford et al., 2004; Forstmeier & Leisler, 2004; Forstmeier et al., 2006; DuBois et al., 2009; mammals: Fischer et al., 2004; Vannoni & McElligott, 2008; Wyman et al., 2008; Koren & Geffen, 2009). Since exclusively females (the mothers) are responsible for parental care and males do not appear to defend resources (they travel while singing; but see Croll, 2002), blue whale songs could indeed function to attract potential mates (Andersson, 1994). Acoustic differences in the structure of songs might therefore be used by females when facing mate choice decisions. The relationships between song, in particular its components, male attributes, and female choice still needs to be elucidated in blue whales. This is also a daunting undertaking considering the difficulty in acquiring individual data and conducting experiments with blue whales in the wild.

Population variability

Song variation at multiple levels of the song structure was also apparent at the population level despite the lack of obvious typological (e.g., use of same units) variations at the beginning of the study. Blue whales from the eastern and western North Atlantic clearly differed in song composition, unit rate, as well as in the acoustic structure of the monotonic unit. Furthermore, there were different trends in the frequency parameters of monotonic units between the two regions, with eastern fundamental frequencies decreasing faster than western ones within the same time span. Blue whales can roam throughout the North Atlantic, but their seasonal movements are not well known. In addition, because of the long-ranging properties of their songs, individuals from different regions within the North Atlantic have the potential to be acoustically and/or physically sympatric (Clark, 1995; Clark & Gagnon, 2004). In such a situation, where animals are likely to be panmictic, song divergence is not necessarily expected (Wilczynski & Ryan, 1999). However, my results show that there is a distinction between eastern and western North Atlantic blue whale songs. Combined with the lack of photographic matches between individuals of the two regions (Sears & Calambokidis, 2002), these findings are in line with (Gambell, 1979), who – based on whaling records – described the existence of two potential North Atlantic blue whale populations. Investigating differences, also subtle ones, in song features can thus provide insights into the structure of populations and help to understand the factors and selective forces driving these behavioural differences. Multiple processes could have accounted for the observed variations, including female preferences for specific song traits, adaptations to acoustic environments or ecological niches, as well as cultural drift (Wilczynski & Ryan, 1999). Furthermore, since blue whale songs are complex signals, different factors could have affected different song traits simultaneously. If linked to a selective advantage, selection for specific traits could be accentuated and result in increasing divergence (Loftus-Hills & Littlejohn, 1992; Howard, 1993; Gerhardt, 1999; Littlejohn, 1999). It is not known if and to which extent assortative mating occurs in North Atlantic blue whales. Genetic analysis could help determining the level of isolation between individuals of the two regions.

Group-specific acoustic variation in sympatrically living individuals of the same species can also result from social factors, and it is mainly driven by vocal learning and vocal traditions (Slater, 1986; Morrice et al., 1994; Deeke et al., 2000; Rendell & Whitehead, 2005). However, this type of group-convergence of acoustic signals is often indicative for species with stable social units, and which rely on group-cohesion when engaged in cooperative

behaviours (Weilgart & Whitehead, 1990; Barrett-Lennard et al., 1996; Wilkinson & Wenrick Boughman, 1998; Crockford et al., 2004). This is not the case with blue whales, but individuals could still use region-specific song traits to maintain loose associations with widely dispersed conspecifics while travelling. Discriminating between conspecifics of different regional "groups" with similar vocalisations might also play an important role in mate choice. This study could not reveal the nature of most of the observed differences, but it puts the basis for further investigations aiming at testing some of the formulated hypothesis.

Context variability

Song variability can also depend on the context and the social environment. Particularly, when many signallers and receivers share the same signalling space, the social environment of an individual can significantly influence signal use. Blue whale males emit infrasonic units either patterned in long sequences, known as songs, or singularly in irregular short sequences referred to as "fragments". Song production is known to be mutually exclusive with feeding (Oleson et al., 2007). By studying patterns of infrasonic unit production in a foraging ground, I found that song emission was not affected by any of the variables describing the social environment, whereas fragment-production depended on the number of females and single whales in close proximity (chapter 3). Furthermore, singing males were travelling, as already reported elsewhere (Oleson et al., 2007), whereas fragments were mainly produced while the animals were engaged in stationary behaviours in relation to feeding, but also to social interactions. This suggests that the social environment and behaviour differentially affected the production of the two types of vocalisations. On the one hand, repeating song elements might be important to increase the locatability of the signaller while moving in a dispersed social environment (Endler, 1992; Bradbury & Vehrencamp, 1998). This would enable distant individuals to track the singer. On the other hand, in a more stationary short-range context, the production of long sequences might be superfluous, because the potential receivers are in close physical and visual range. Alternatively, the presence of close females might have suppressed singing activity (Oleson et al., 2007) as shown in many species that use vocal displays as mate attraction signals (e.g., Breitwisch & Whitesides, 1987; Catchpole & Slater, 1995; Dunn & Zann, 1996; Mitra Setia & van Schaik, 2007). This hypothesis is further supported by the fact that travelling singers were solitary, not in visual contact with other individuals. Furthermore, I found that in all the cases in which fragments were produced, females were always present, in 80% also pairs, but not necessarily other single males. This further suggests that song units are involved in inter-sexual interaction. Since individual

differences are present in the composition, and temporal structure of songs as well as in the acoustic structure of monotonic units, both songs and fragments might be used to identify, assess and potentially recognise individuals. Since songs appear to be undirected, differences at multiple levels of their structure might ensure that information about the individual is transmitted also at a distance. More detailed studies are required to assess these relationships as well as the use of patterns of song unit sequences in individual cases.

Anthropogenic noise and call variability

Variations in vocal behaviour are not only common in natural contexts, but can also occur as a response to activities that interfere with acoustic communication. Anthropogenic noise for instance can mask acoustic signals and induce behavioural changes for coping with such interference (Richardson et al., 1995; Brumm et al., 2004; Slabbekoorn & Peet, 2003). Studying compensatory acoustic responses of noise interference is not only important to investigate vocal plasticity and short-term adjustments, but also to determine the ranges at which noise might affect communication, and thus animal groups. This has implications also for management and conservation, since changes in the acoustic behaviour as a function of noise can be stressful and costly (Rabin et al., 2003). Blue whales are highly vocal, and besides producing infrasonic sounds that compose their songs, both sexes also emit higher-frequency, transient calls that mainly occur singly and sometimes in bouts (Di Iorio, unpublished data). Calls are emitted during social interactions and feeding (Berchok et al., 2006; Oleson et al., 2007). Because of their acoustic structure, calls are likely to be affected by pulsive noise as from seismic surveys. I found that call production was consistently higher in presence than in absence of seismic survey activity (chapter 4). The exposed animals were presumably compensating for the increase in ambient noise from seismic survey activity. Since the response was observed at relatively low received levels, the ranges at which seismic noise affects a whale's behaviour, might be larger than previously assumed (Southall et al., 2007).

Although it would have been interesting to also investigate how the production of songs was affected by seismic noise, this was not possible because blue whales start to emit infrasonic song units only towards the end of the summer, when the survey had already taken place. However, observations in earlier reports described a cessation of singing when blue whales were exposed to seismic survey activity (McDonald et al., 1995; Clark & Gagnon, 2004). These opposite responses might be linked to the context (socialising vs. travelling) as

well as to the communication-range of the signals. Songs are used for long-range communication, they are highly redundant and can last up to days. In accordance with the observation by McDonald and colleagues (1995), a travelling male could restart singing once the noise level decreases, and thus restore the temporary loss of information. In contrast, calls are transient, discrete, non-patterned, and not as frequently emitted as songs (Oleson et al., 2007). There might thus be a different pressure with regard to the transmission of information that is usually coded in a non-redundant signal in a socially relevant situation. In this case, an increase in the production of calls could reduce the masking of information by noise (Shannon & Weaver, 1949). Although the study could not show a compensatory response at the individual level, the clear results are in line with this explanation. These findings also show that anthropogenic noise can differentially affect vocal communication. It also emphasises the importance of evaluating the duration of the interference as well as the behavioural context, the type and functional significance of the vocalisations potentially affected.

Conclusions

Altogether, the three studies on song variability reveal that songs are primarily directed towards females and they strengthen the evidence that blue whale songs are reproductive displays. This work also shows that blue whale songs are complex signals that might have evolved, and still do, to provide more reliable information to receivers at the individual and the geographical level, as well as a consequence of a variable environment. Furthermore, it points out that studying variation in the acoustic signals at different levels of the signal structure and the network environment provides a more global picture of patterns of variability and thus the factors shaping the signals. This is particularly important when experimental studies cannot be carried out due to the difficulty of working with species such as the blue whale. This study also reveals that blue whales show short-term reactions in their vocal behaviour in response to interfering noise and that such behavioural changes might differ depending on the communicative value of the signals and contexts in which they are emitted. This further stresses the importance of studying contextual use, function and natural variability in acoustic signals.

Since communication and social behaviour are tightly linked, this thesis also augments our knowledge of the blue whale's sociobiology. Comparisons with other, in particular better studied terrestrial organisms can be very enlightening to this respect. Many of the points I will mention probably also apply to other Balaenopterid whale species such as the humpback

(*Megaptera novaeangliae*), the fin (*Balaenoptera physalus*) or the minke (*Balaenoptera acutorostrata*) whale among others, and some explanations have been proposed for humpback whales too (Clapham, 1996). However, blue whales differ in multiple ways from other closely-related species. For example, they do not appear to have defined breeding grounds in temperate waters such as humpback whales do and they feed exclusively on krill unlike all other Balaenopterid species that also feed on schooling fish. Therefore, blue whales do not show any kind of co-operative feeding behaviour as sometimes observed in humpback or fin whales.

Other non-territorial or widely ranging species that have a highly fluid social system and also emit long-distance signals for social communication include elephants, chimpanzees and dolphins. These animals live in fission-fusion societies in which individuals, or in the case of elephants also groups, regularly associate in parties (c.f., Couzin, 2006). Fission-fusion societies are stable social units in which individual group members are often found alone or in small subgroups and in which subgroup size and composition change frequently over time (Kummer, 1971; Smith et al., 2008). Therefore, contrarily to species with strong group cohesion that show convergence in acoustic signals (e.g., Ford, 1991; Weilgart & Whitehead, 1997), individual vocal identity is favoured in fission-fusion societies. In fact, identifying and recognising a specific individual plays an important role when initiating reunions, when maintaining spatial contact between dispersed party members, or when mediating individual-specific interactions from a distance (Mitani & Nishida, 1993; McComb et al., 2000; Janik et al., 2006). The main reasons for individuals to fuse are mainly linked to ecological or social benefits such as predator avoidance, exploitation or defence of resources such as food or mates, reduced risk of harassment, or social learning (van Schaik, 1999; Connor et al., 2000; Smith et al., 2008; Clutton-Brock, 2009). Furthermore, the aforementioned species are all gregarious.

Blue whales are not gregarious, they do not have easily recognisable social units and are mainly found singly, often in pairs or in small loose associations (Sears & Calambokidis, 2002). Furthermore, predation pressure is assumed to be relatively low (25% of blue whales have scars from orca attacks), and no cooperative behaviour such as group-defence, group-foraging, or group-care of offsprings are known to occur in this species (Gambell, 1979; Sears & Calambokidis, 2002; Sears, 2008). However, congregations of mother-calf pairs have been observed in blue whales in coastal areas (Hucke-Gaete et al., 2004) but we ignore whether they are random or whether females in the same reproductive condition may profit from

associating during the short (six to eight months) waning period (e.g., for offspring defence). Therefore, the principal reason why dispersed blue whales should associate and coordinate conspecifics in time and space is likely linked to social benefits such as reproduction. The emission of individually-distinct songs during the long-range movements appears to be the best means to mediate such interactions, particularly considering it's potential role in mate-attraction. Large aggregations of blue whales can occur in feeding areas, where food abundance is very high (Sears & Calambokidis, 2002). Blue whales may benefit from these temporary congregations since they represent low-cost opportunities for social interactions and mate choice (chapter 3). Since the extensive roaming of blue whales is thought to be driven by food requirements (Moore et al., 2002; Clark & Gagnon, 2004), singing while travelling between food patches might facilitate such temporary reunions. This hypothesis concords with Croll and colleague's (2002) suggestion that fin whales sing to attract, I would also add direct, females to food aggregations. Altogether, this suggests that blue whale have an individual-based highly fluid fission-fusion system that shares little characteristics with the above mentioned species, but several with another semi-solitary mammal species, the orangutan (Delgado & Van Schaik, 2000). Although many differences are present, in terms of social structure, slower life history of orangutan females, or cultural transmission among others, the factors affecting fusions or larger aggregations appear to be very similar, as well as the main function of the male's long-distance calls, that in both cases are likely to be mainly directed at females in order to attract them.

In conclusion, the blue whale is a system with characteristics that appear to be unique, maybe linked to its ocean basin-wide physical and acoustic ranging in an environment that sets no major natural constraints.

"The limits of my language mean the limits of my world." L. Wittgenstein

Future Research

This study sheds light on various aspects of the vocal signalling and sociobiology of one of the most cryptic animal species. It contributes to a better understanding of the potential function and role of long-range signalling in species living in very vast and fluid social environments. It also shows how patterns of variability in vocalisations can contribute to

better comprehend behavioural changes and provides new insight into potential evolutionary mechanisms shaping acoustic signals in a system that lives in a highly variable socio-ecological context. As often in science, this study opens up new questions and hypothesis that ask to be answered. It would be important for instance to record the same males multiple times within a season and between years in order to study individual variability or stability of the different song components. This would be feasible in the St Lawrence with the frequent visitors such as 'Popeye' or 'Torishinto' and very important to emphasise the use of songs. Moreover, stable song features could serve to count singers in remote areas and thus enable a better estimate of population sizes (of the males at least) over the years. This study also provides the basis for further investigating geographical differences and the distinct trends observed between the blue whales of the two geographical regions. An interesting study would be to further test the hypothesis of species competition for the same acoustic channel. For this purpose comparisons should be made between different areas within the North Atlantic, in particular in the western part, with a high presence of fin whales using recordings from different years in order to control for the effect of years. This could be done using passive acoustic recordings available since over ten years (Clark, 1995). For a better understanding of the influence of the social environment as well of anthropogenic noise on blue whales, acoustic tags placed on the animals would be very helpful, as already shown in multiple studies (Johnson & Tyack, 2003; Oleson et al., 2007). Their application would enable to observe individual behavioural changes in movements and acoustic behaviour. Although it is difficult to measure blue whale male attributes, one cue that could be measured using digital photography is size (Dawson et al., 1995). It has never been tested on blue whales but it would be worth trying it, particularly in conjunction with recordings from acoustic tags. Finally, genetic analysis would help elucidating many of the relationships addressed in this thesis, as for example in conjunction with the geographical differences found, or to assess paternities. This would however be a difficult undertaking with the St Lawrence population because very few calves (ca. 16) have been sighted over the last 30 years (Ramp et al., 2006). Nevertheless, in areas with more mother-calf pair sightings such as in Baja California, Chile or Iceland it could be investigated, although only together with a representative sampling of potential fathers. Genetic analysis, particularly of kinship, could also be useful in getting a better insight into the social structure of blue whales. During the years spent in the St Lawrence, patterns of associations emerged from personal observations, in particular among females. Available long-term photo-id data combined with genetic analysis could serve to investigate these suppositions. Finally, in terms of female choice experiments, we need to wait for more advanced technologies to produce these very low and

intense blue whale songs, and even if such technology was available, it would remain a difficult endeavour, also considering the signalling ranges and thus the potential audience.

Last but first, the present study is situated at the interface between behavioural ecology and conservation biology. Combining these two fields is fundamental for a better evaluation of management procedures. This is particularly relevant in the case of endangered species such as the blue whale that faces a high risk of extinction (IUCN, 2008)

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